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New Sea Temperature Measuring Devices

By

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I. A Temperature-Depth Recorder

The temperature-depth recorder was developed to fulfil the requirement of the Hydrographic Section of the Fisheries Laboratory, Lowestoft, for a device to measure rapidly and accurately the variation of temperature with depth in ocean waters.

A general specification for the equipment was laid down as a guide for the design:—

1. The final record to be in the form of a continuous graphed paper roll with inked trace.
2. The influence of roll and pitch to be negligible.
3. The overall accuracy of temperature and depth measurement to be of the order $\pm 1\%$ of full-scale deflection.
4. The equipment to be capable of simple modification to allow alternative ranges of temperature and depth to be measured if desired.
5. After initial set-up, the equipment to be automatic in recording.
6. The equipment to be capable of withstanding the rough usage normally associated with shipborne apparatus.

The following is an account of a prototype instrument designed to the above specification and used continuously over a period of a month at sea on the R/V "Ernest Holt" during the Faroe-Iceland Ridge survey (May–June, 1960) organized by the International Council for the Exploration of the Sea.

Basic Principle

To achieve maximum simplicity and reliability it was decided during the early stages of design to use a d.c. system and incorporate a standard Honeywell Brown Chart Function Plotter (x.y. Recorder). This device has two completely independent circuits for measuring two separate variables. The pen records one variable (x) as distance across the width of the chart and the other variable (y) as distance along the length of the chart. Thus the curve that the pen draws

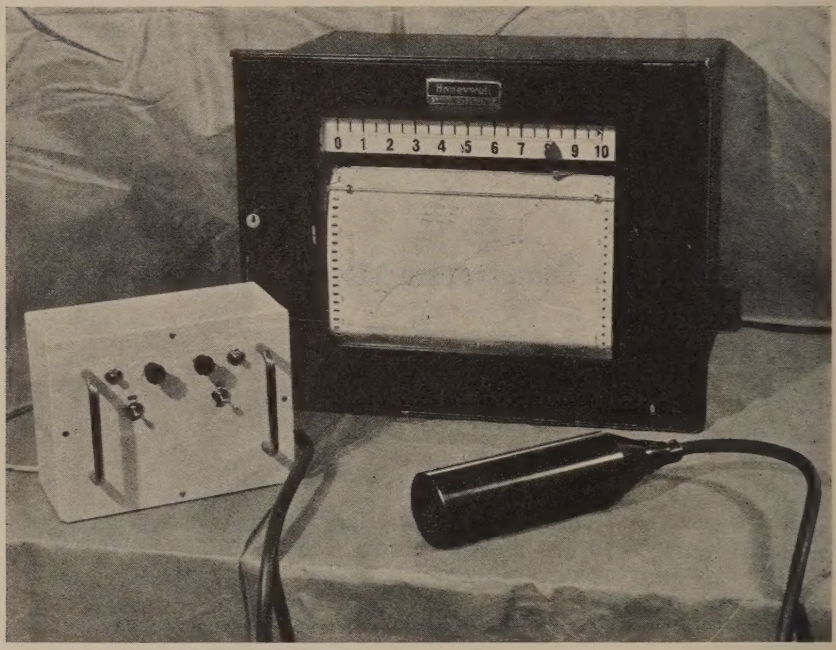

Figure 1. The temperature-depth recorder.

represents the function of one of the variables in terms of the other (Temperature-Depth). The two variables require d.c. inputs of 10 millivolts for full-scale deflection. This represents 27·9 cm (11 in.) of chart in both the horizontal and vertical directions. The paper chart is a continuous roll made up as a series of 11 inch linear graphed squares: each 27·9 cm (11 in.) scale is divided into tenths and hundredths.

The measurement of temperature is achieved by using a thermistor connected in one arm of a Wheatstone bridge arrangement. The bridge is supplied with constant voltage direct current, and variation in temperature of the thermistor causes a resistance change and unbalances the bridge. This out of balance voltage is fed to the Honeywell Brown recorder, thus giving a deflection of the (x) axis. The measurement of depth is achieved by using a precision pressure transducer energized by a stable d.c. voltage, measuring pressure as a function of depth. The out of balance signal from the pressure transducer is fed into the Honeywell Brown recorder, thus giving a deflection of the (y) axis.

The pressure transducer and thermistor were accommodated in a watertight housing and connected to the recording equipment through a 550 m length of cable. The cable was designed with a central steel strain strand capable of withstanding the combined weight of the underwater unit and cable. Figure 1 shows the complete apparatus. The Honeywell Brown recorder is in the background, showing a typical temperature-depth profile on the paper chart; in the foreground is the temperature-depth sensing unit and the control box.

Design

(i) Depth measuring circuit

A precision pressure transducer (Solartron type MT. 4313) is incorporated in the underwater sensing unit and measures depth in terms of pressure. The pressure transducer is an unbonded strain gauge comprising a four arm Wheatstone bridge, R_{abcd}. The bridge circuit is constructed of platinum alloy strain wires wound on insulating posts. Two active arms are wound around a rhomboidal section, with the two inactive arms wound around the base-mounted pins. When pressure is applied to the pick up diaphragm the deflection of the diaphragm is transmitted through a star element to the active strain wires, thus causing a change in resistance which unbalances the bridge circuit.

The resultant electrical output is precisely proportional to the applied pressure. It will also be apparent that the output voltage is proportional to the input voltage and it is therefore of paramount importance to maintain the energizing voltage constant under all conditions.

Acceleration and vibration have little net effect on the output, since they are cancelled by the geometry and winding arrangement of the star spring element. Close proximity of the active and inactive windings ensures a common thermal environment, thus considerably minimizing any effects of temperature change.

The transducer is energized by a stabilized power supply (Solartron Power Supply type AS958) operating from the ship's alternating current mains (Fig. 2). The energizing voltage V_d is controlled in amplitude by R_{cd}, which is the calibrating potentiometer. R_{cd} is preset when the equipment is calibrated and is not touched until recalibration is necessary.

The transducer bridge arms were approximately 350 ohms and, with an excitation of 5 V, resulted in a current drain of approximately 15 milliamps. With this small current drain batteries may be used in place of the stabilized power supply provided that a means of checking the applied bridge voltage (V_d) (and hence the calibration) is incorporated. (An earlier model was developed and worked satisfactorily with batteries.) The zeroing potentiometer R_Z adjusts for any resistance out of balance in either the transducer (R_{abcd}) or the underwater cable ($R_{c\ 1\cdot2\cdot3\cdot4}$) and is adjusted only under "zero pressure conditions".

Calibration of the depth measuring circuit was effected by subjecting the underwater unit containing the transducer to a series of pressures equivalent to the head of water being measured. With the maximum pressure equivalent to the greatest head of water (500 m in this case) R_{cd} was adjusted so that the out of balance voltage supplied to the Honeywell Brown recorder was precisely 10 millivolts. Check points were then determined at lesser pressures. The relation between head of water and deflection of the paper chart (millivolts) is linear.

(ii) The temperature measuring circuit

The temperature measuring element is a glass encapsulated thermistor (Standard Telephone and Cables Thermistor type F2300) which is connected in one arm of a Wheatstone bridge network. Figure 2 shows the basic circuit diagram. A stabilized direct current voltage (V_t) is supplied to the Wheatstone

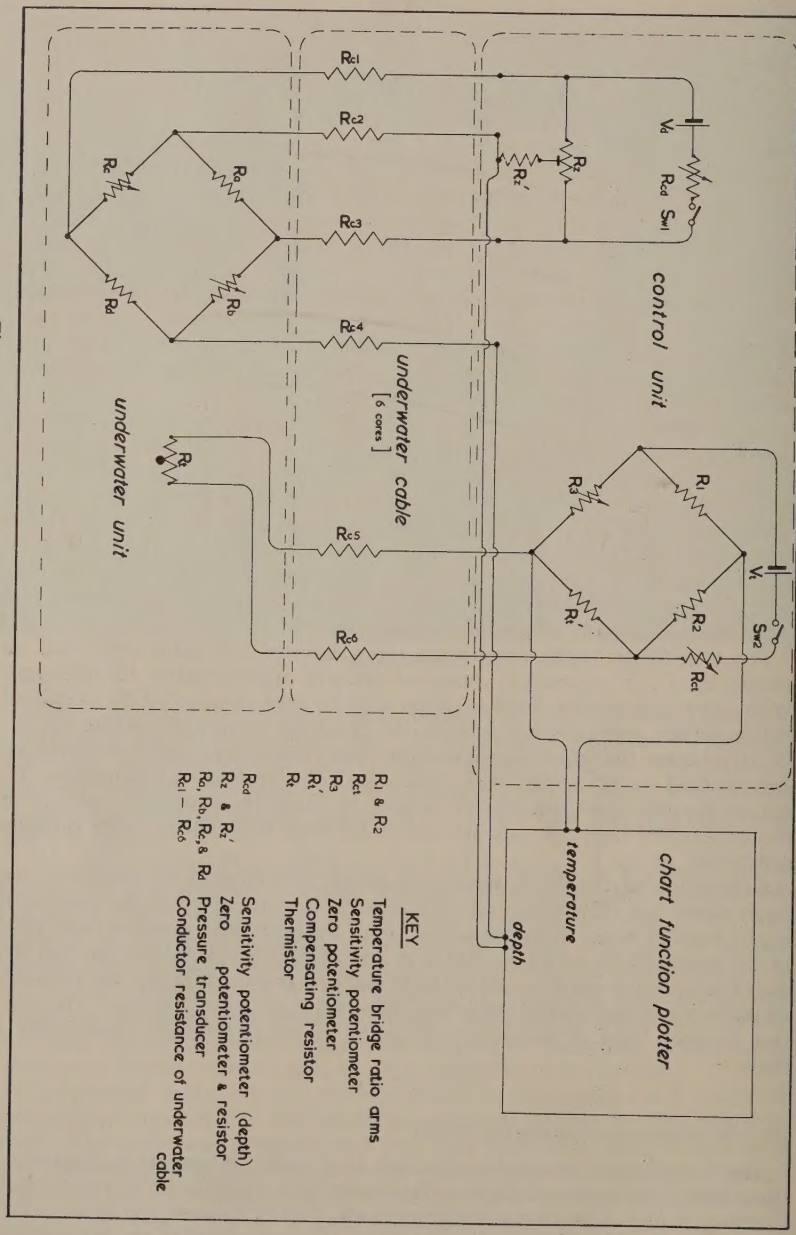

Figure 2. Basic circuit diagram of the temperature-depth recorder.

bridge via switch Sw_2 and potentiometer R_{ct}. R_{ct} is the calibrating potentiometer and adjusts the bridge supply voltage. R_1 and R_2 are the ratio arm resistors, which are equal in value. R_3 is the zeroing potentiometer which balances the bridge at the lowest end of the temperature range. The fourth arm of the bridge is made up with the combined resistance of R'_t, R_t, R_{c5}, R_{c6} where:—

R_t = Thermistor resistance
R'_t = Compensating resistance
R_{c5}, R_{c6} = Conductor resistance of underwater cable.

Change of temperature results in a change of thermistor resistance (R_t) thus unbalancing the bridge network and causing an out of balance potential at the recorder terminals. The compensating resistor (R'_t) shunting the thermistor, enables a substantially linear relation between temperature and millivolts deflection to be obtained.

Typical design values are:—

Thermistor resistance at 0°C = 4580 Ω
at 10°C = 3100 Ω
$R_1 = R_2$ = 2·2 KΩ
R'_t = 3·7 KΩ
$V_t \simeq$ 1 Volt.

Calibration of the temperature measuring circuit was effected by immersing the underwater unit in water at 0°C and adjusting R_3 for balance conditions (i.e. 0 mV = 0°C). Water temperature was then raised to 10°C, where R_{ct} was adjusted so that the Honeywell Brown recorder was reading 10 mV (10 mV = 10°C). Spot checks were then made at temperatures between these values.

The arrangement works quite well with batteries provided that a calibrating circuit is added. This method is used quite satisfactorily in temperature measuring apparatus of a similar nature.

It is necessary to check that the thermistor has been correctly encapsulated in araldite epoxy resin so that the effect of pressure on the thermistor is negligible. The thermistor assembly is subjected to increasing pressures up to a maximum of 56·2 kg/cm² (800 P.S.I.) for this model. For correct encapsulation the thermistor bead only should be showing above the level of araldite. Too little araldite results in the thermistor becoming pressure sensitive at higher values of pressure, whilst too much araldite covers the thermistor bead and increases the thermal time constant.

(iii) The underwater unit and cable

Figure 3 shows an exploded view of the underwater unit containing the thermistor and pressure transducer, which are shown in greater detail in Figure 4. The underwater unit was designed to allow rapid dismantling and easy replacement of the thermistor and transducer. To achieve this, all pressure seals, other than the cable gland entry, were of O ring construction. The cable gland, once tightened, should not have to be touched until replacement of the

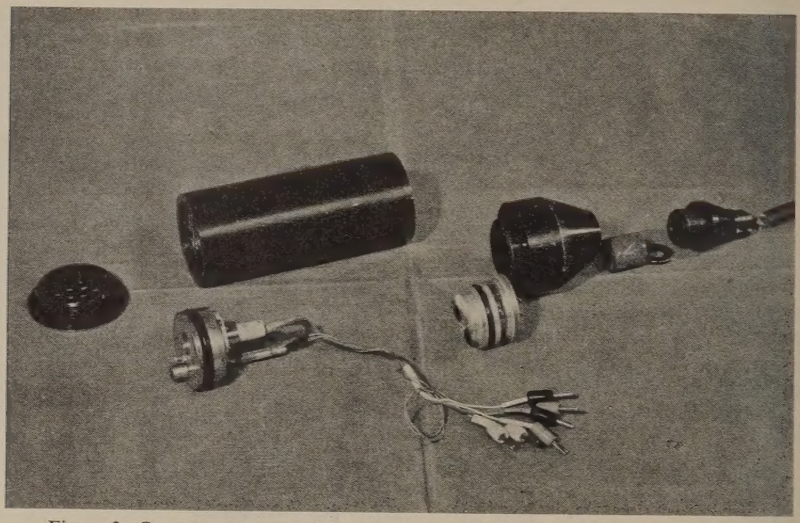

Figure 3. Component parts of the temperature-depth recorder underwater unit.

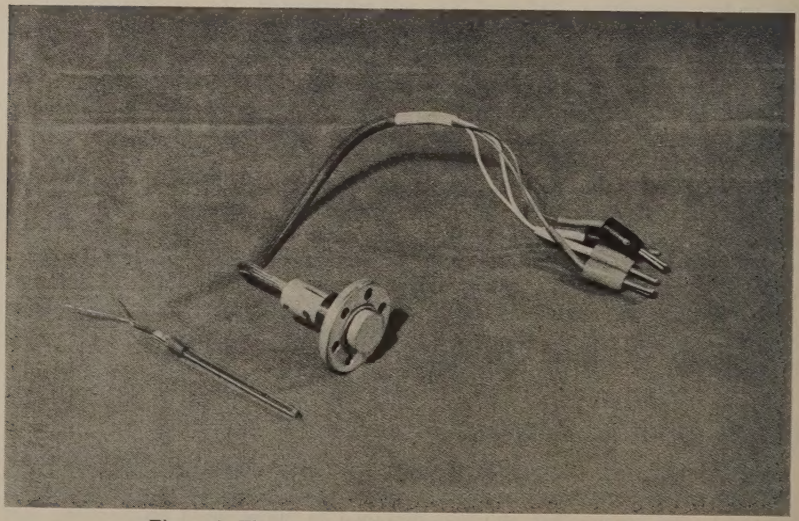

Figure 4. The pressure transducer and thermistor of the temperature-depth recorder.

cable becomes necessary. All other adjustments and replacements, etc. can be effected from the front end of the instrument.

The thermistor is encapsulated in a brass tube with araldite, the brass tube first being soft soldered into the front bulkhead. This bulkhead also carries the pressure transducer which is screwed home on to an O ring seal. The electrical leads from this assembly are plugged into sockets in the rear bulkhead, and the whole assembly slides into the underwater unit pressure housing. The front cover is then screwed on, and, when tightened, forces the front bulkhead against a shoulder on the main housing, thus ensuring that the O seal is located correctly to form a watertight joint. The front cover also prevents any mechanical damage to the thermistor and transducer. Before final assembly the whole of the interior of the underwater unit, especially electrical connections and O seals, is liberally smeared with silicone grease. This assists the sealing properties of the seals O and also prevents the development of low resistance leakage paths due to moisture forming on the inside of the unit.

The underwater unit was designed for use at pressures between 0 and 70·3 kg/cm^2 (0 and 1000 P.S.I.) but provision can be made for it to be oil filled, with a compensating pressure element between the oil and sea water, to effect a balance of pressure. The loss of pressure differential has no effect on the pressure transducer, since this unit is in itself completely sealed.

Due to material delivery problems the underwater unit was manufactured from Duralumin and then anodized to prevent corrosion. This reduced its effective weight, and additional weight was added to allow it to fall as near the vertical as possible as quickly as possible. With the underwater unit manufactured from brass or phosphor-bronze, as was originally intended, it should not be necessary to attach extra weight.

The cable for the temperature-depth recorder is a specially designed 6 conductor cable with a separate steel strain bearer (itself PVC insulated). The six conductors are laid round the central steel strain bearer, proofed, taped, heavy duty tough rubber sheathed, canvas reinforced and finally heavy duty rubber sheathed, the overall diameter of the cable being approximately 1·3 cm (0·5 in.). The weight is about 178 kg (3½ cwt) per 914 m (1000 yds) and the breaking strain is 499 kg (1,100 lb). It is of paramount importance to have a longitudinally "stiff" cable, otherwise stretch occurs and individual conductor resistance increases. These increases of resistance are seldom equal in all conductors, and errors become appreciable in depth and temperature measurement. Rubber covered cables are essential when the equipment is likely to be used in cold or arctic waters, where the plastic cables at present available become exceptionally stiff and unmanageable.

Laboratory Tests

Before the initial sea trials were due to take place the temperature-depth recorder was calibrated. The results of this calibration are shown in Table 1.

For the purpose of accurate calibration the temperature standard was a mercury and glass secondary reference thermometer calibrated by the National Physical Laboratory and capable of being read to one hundredth of a degree centigrade. The pressure standard was a Budenberg precision pressure gauge 70·3 kg/cm^2 (0–1000 P.S.I.) accurate to within 0·25% of full-scale deflection.

Table 1

Calibration: 18. May 1960

True temperature (°C)	Indicated temperature 1 mV ≡ 1°C	True depth (m)	Indicated depth (m) (1 mV ≡ 50 m) Down	Up
0	0	0	0	0·2
2·00	1·98	100	98·0	99·0
4·00	3·97	200	197·5	198·0
6·00	5·97	300	297·5	298·0
8·00	7·98	400	397·5	398·0
10·00	10·00	500	498·0	498·0

Table 2

Calibration: 29. June 1960

True temperature (°C)	Indicated temperature 1 mV ≡ 1°C	True depth (m)	Indicated depth (m) (1 mV ≡ 50 m) Down	Up
0	0	0	0	0
2·00	1·98	100	98	98
4·00	3·96	200	200	200
6.00	5·96	300	298	298
8·00	7·98	400	398	397
10·00	10·00	500	500	500

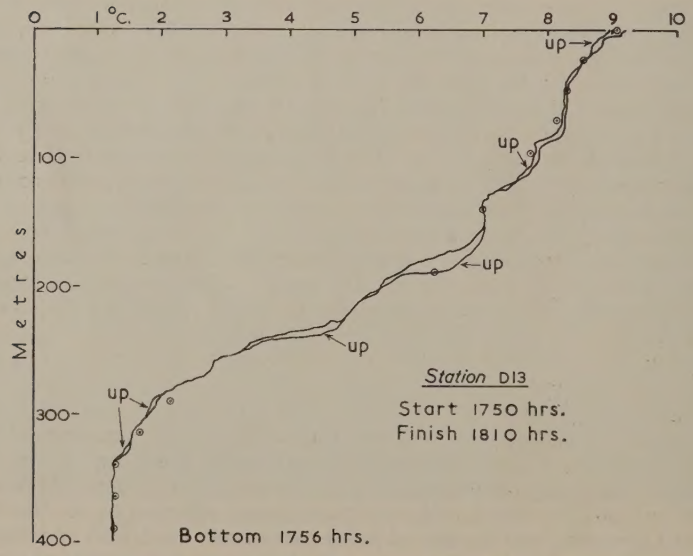

Figure 5. Typical temperature and depth profile, showing close agreement with water-bottle temperatures.

After sea trials which entailed lowerings at 50 stations the temperature-depth recorder was recalibrated. The results of the calibration, given in Table 2 show that the overall accuracy of temperature and depth measurement was better than $\pm 1\%$ of full-scale deflection. The long-term stability of the temperature and depth measuring circuits is shown by Tables 1 and 2. The maximum drift between temperature calibration (1) and (2) was 0·01°C, which agrees with previous experience obtained by long-term stability tests with this type of thermistor.

The maximum drift between depth calibrations was 2 m in 500 m.

Discussion

During the Iceland-Faroe Ridge survey mentioned earlier the instrument was used at 50 stations and worked satisfactorily. It was found that the temperature-depth recorder is capable of giving consistently rapid and accurate profiles of temperature and depth. The equipment was trouble free throughout the survey and gave consistently good results even during conditions of heavy swell. When lowerings are attempted under such conditions the profile becomes "swell modulated", i.e. the equipment becomes an efficient wave recorder, and the temperature-depth profile is modulated by the swell action. A logical development, if the equipment were desired to measure temperature-depth profiles under consistently heavy swell conditions, would be the inclusion of a simple filter. However, this is not necessary under normal conditions of operation.

After initially switching on and giving time to warm up (about 10 mins.), the cable was allowed to fall freely until the required depth was obtained. This, of course, automatically recorded the "down" profile. The cable was then hauled up by means of the whipping drum on the main winch of the "Ernest Holt", thus giving the "up" profile.

A useful accessory for the temperature-depth recorder would be a small electric winch equipped with slip rings and mounted close to the rail of the vessel. This would allow more rapid lowerings and do away with the necessity of handling and coiling down the electric cable as it came inboard. Arrangements are being made for such winches to be installed on the new R.V. "Clione", at present in commission.

Figure 5 shows a typical temperature-depth profile obtained at Station D13 during the survey. Temperatures obtained with pairs of reversing thermometers carried on Nansen water bottles are superimposed on the profile and show good agreement with it. Station D13 was located at 63°23′N, 11°19′W, near the top of the Faroe-Iceland Ridge and on its south-western side in 403 m depth. The profile shows that cold bottom water with a temperature of about 1·2°C was overflowing the Ridge at this point and that the over-spilling water was homogeneous for some 60 m above the bottom. The surface temperature was about 9°C and the profile shows that the temperature was not decreasing smoothly from surface to bottom, but in a series of steps. The divergence between the "down" and the "up" profiles is not due to hysteresis in the instrument, but to a change in water temperature during the 20 minutes required to make a lowering and hoisting: this change may have been partly the result of the ship's drift and partly the effect of internal waves.

II. A Portable Thermistor Thermometer

This instrument was developed following requests from various trawler skippers and owners for a device that would be capable of giving instantaneous readings of sea temperatures at depths ranging from surface to 366 m (200 fms). The range of temperatures likely to be encountered would be from −2°C to +18°C. The instrument would be operated by non-scientific personnel and would therefore have to be simple to operate and require a minimum of adjustment and maintenance.

It was realized that the proposed instrument would also be useful for certain aspects of marine research, and so it was decided to design the thermistor thermometer to give a somewhat higher degree of accuracy than would normally be required for the day to day measurement of sea temperatures for fishing.

To cover the required temperature range it was decided to design two models, an arctic model of temperature range −2°C to +8°C, and a North Sea model of temperature range 8° to 18°C (i.e. both with a range of 10°C). The basic design of the two models would be identical but circuit values (resistance) would of course differ.

An overall accuracy of ±1% of full-scale deflection was desirable.

Description of the Apparatus

Figure 6 shows the complete apparatus in its carrying box. The temperature sensing head, containing the thermistor, is joined to the control box by a length of twin core tough rubber sheath cable. In the prototype model shown a cable length of 91 m (100 yds) was used but this length can be modified at will. It is, however, necessary to compensate the electrical circuit for any appreciable change in conductor resistance of the cable.

The control box contains the electrical circuit, together with the battery and moving coil meter calibrated directly in °C.

Design

The basic circuit is shown in Figure 7 and is a Wheatstone bridge arrangement with a thermistor (Standard Telephone and Cables type F2300) in the variable arm. The detector is a micro-ammeter (0–100 micro-amps) which is calibrated directly in °C. The bridge is energized by a 4 V mercury cell (3 off Mallory type RM12R) through the on/off switch Sw_1 and the calibrating potentiometer R_{ct}. The resistors R_1 and R_2 are the ratio arms of the bridge and in this design are 2·2 KΩ in value. A "Press to Calibrate" switch Sw_2 switches into the circuit a calibrating arm whose resistance (R_{cp}) is equal to the combined cable and thermistor resistance at the maximum temperature on the meter scale: (8°C in the arctic model and 18°C in the North Sea model). The remaining arm of the bridge contains the zeroing potentiometer R_Z which allows the bridge to be balanced at the low temperature end. The bridge is arranged so that it is in balance when the thermistor is at its lowest temperature (i.e., −2°C in the arctic model and +8°C in the North Sea model). It is essential that the thermistor connecting cable is attached when adjustments are made to the bridge circuit, as the conductor resistance $R_{c1} + R_{c2}$ is part of the thermistor arm resistance. The thermistor is then placed in water of temperature equal to the

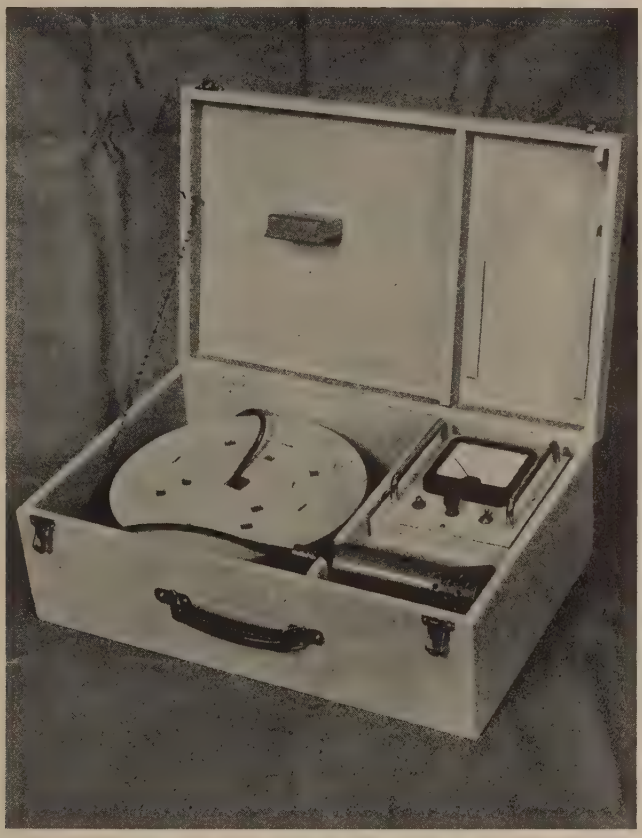

Figure 6. Complete thermistor thermometer equipment in carrying box.

highest temperature to be measured (+8°C in the arctic model and +18°C in the North Sea model) and R_{ct} is adjusted so that the micro-ammeter reads 100 micro-amps. The "Press to Calibrate" switch is now operated and the preset potentiometer R_{cp} is adjusted so that the micro-ammeter reads 100 micro-amps. This ensures that the resistance of the calibrating arm is identical with that of the thermistor arm and can be switched into circuit at will to check either the battery voltage or the functioning of the thermistor circuit.

Falling battery voltage is compensated by pressing the "Press to Calibrate" switch and adjusting the micro-ammeter for full-scale deflection by means of calibrating potentiometer R_{ct}. Release of the "Press to Calibrate" switch puts the thermistor arm back into circuit and the meter then reads temperature.

The mercury cell was chosen for its excellent discharge characteristic. The terminal volts are very nearly constant until the battery is practically exhausted, when the terminal volts drop quickly. With this characteristic the "Press to

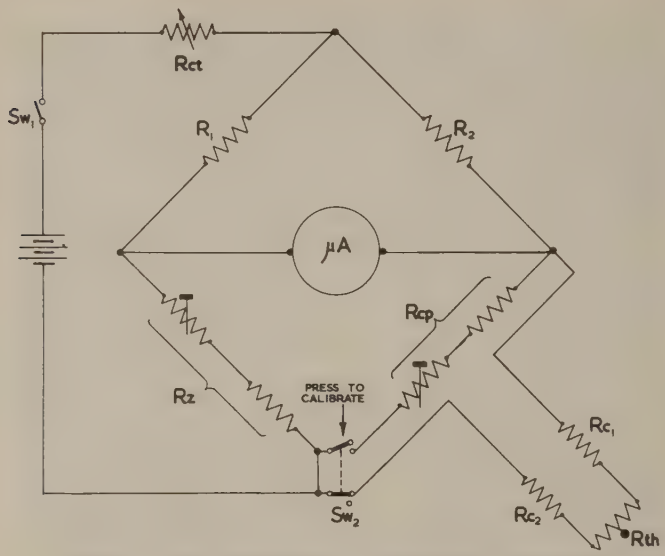

Figure 7. Basic circuit diagram of the thermistor thermometer.

Calibrate" operation is necessary only after some hours of continuous temperature measurements. Mercury cells in some of the thermistor thermometers in use at the Fisheries Laboratory, Lowestoft, have been in use for up to nine months before requiring replacement.

Temperature Sensing Head

The construction of the prototype temperature sensing head is shown in Figure 8. It is necessary for the sensing head to be sufficiently heavy, so that when measuring temperatures at some considerable depth it falls through the water as rapidly as possible, thus permitting it to reach its maximum depth and reduce any tendency to stream. To achieve this and also to prevent corrosion taking place, the sensing head is manufactured from phosphor-bronze.

The thermistor is encapsulated into its holder (A) with araldite adhesive resin, so that only the temperature-sensitive bead is showing above the araldite. The thermistor holder is then offered into the main body of the sensing head and pulled home against its O seal by means of the circular nut (B). To protect the thermistor from mechanical damage a cover (C) screws on to the main body (D) of the sensing head and projects slightly ahead of the thermistor bead. The wires from the thermistor are soldered to the terminal disc (E), and at the same time the underwater cable is fed through the end plug (I), the washer (H), the rubber gland (G), and the rear portion of the sensing head (F), and soldered to the terminal disc. The front and rear portions of the sensing head are then tightened, and the rubber gland, washer, and end plug screwed fully home. This

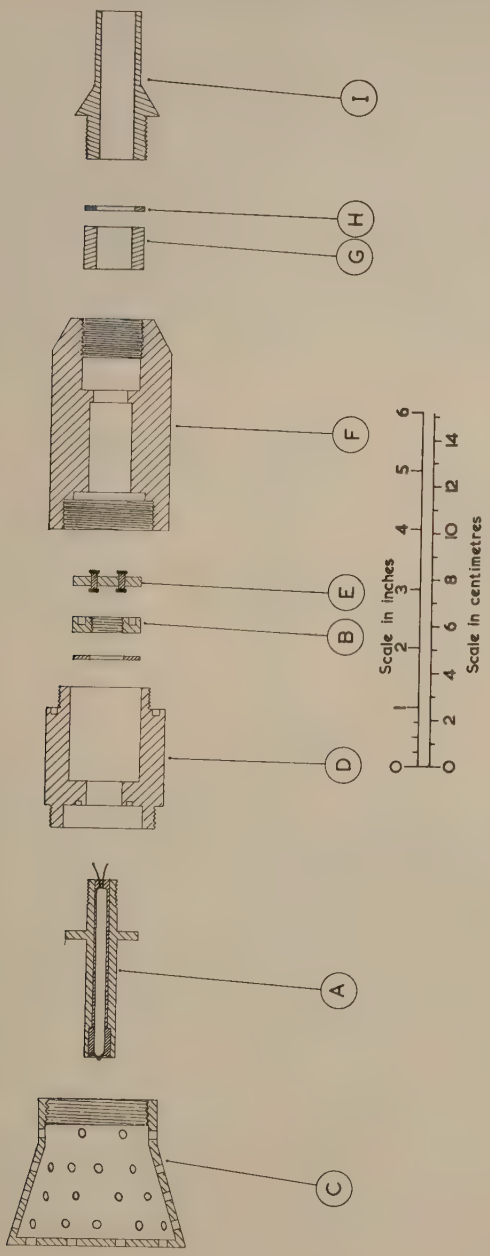

Figure 8. Temperature sensing head of the thermistor thermometer.

arrangement gives a watertight casing suitable for use at pressures up to 70·3 kg/cm^2 (1,000 P.S.I.) and facilitates simple replacement of the thermistor holder unit.

Calibration

A typical calibration of a Thermistor thermometer against an NPL calibrated secondary reference Mercury in Glass thermometer is shown in Table 3.

The Thermistor thermometer is calibrated by immersing the temperature-sensitive head in water which is stirred continuously. Starting at the lowest temperature, warm water is gradually added and readings of the Mercury in Glass thermometer, which is also immersed in the water bath, are compared with the deflection on the micro-ammeter at a number of points along the temperature scale.

Table 3

Mercury in Glass thermometer T_1 (°C)	Corrected temperature T_2 (°C)	Thermistor thermometer 10 micro-amps ≡ 1°C
8·230	8·260	8·30
9·590	9·615	9·62
11·015	11·045	11·05
12·440	12·470	12·47
13·540	13·570	13·57
14·470	14·505	14·50
15·425	15·460	15·45
16·550	16·580	16·60
17·160	17·185	17·22
17·900	17·920	18·00

Discussion

The relation between temperature and deflection of the meter is substantially linear and the meter does not require separate calibration. The overall accuracy of temperature measurement is better than $\pm 1\%$ for the range of 10°C, i.e. $\pm 0{\cdot}1$°C. However, it should be appreciated that for different scale ranges this accuracy may not always be obtainable, due to difficulty in correcting for the thermistor characteristic.

A thermistor thermometer of temperature range −2°C to +23°C (25° range) has been developed for the remote measurement of condenser intake water in ships. This device has an accuracy of $\pm 0{\cdot}25$°C throughout the 25°C range. The first prototype model was fitted to the R/V "Ernest Holt" in September 1959 and has given trouble free service. This particular thermistor thermometer was recalibrated when the batteries were renewed after approximately nine months' use, and the difference in calibrations was negligible.

A comprehensive series of tests (MAFF 1960 Internal Report: "To determine the effect of warm outlet water on the cool sea water entering the condenser intake of a ship".) was recently conducted on the Ocean Weather Ship "Weather Adviser" to prove that the measurement of condenser inlet water temperature was an accurate and reliable measurement of sea temperature at the depth of the condenser intake. The results of these tests were satisfactory and thermistor

thermometers will therefore be fitted in the condenser intake of certain other ships for the measurement of sea temperature.

A number of thermistor thermometers of various temperature ranges have been manufactured at the Fisheries Laboratory. These instruments have been used in many forms of fishery and hydrographic investigations and proved extremely reliable. They have been used for the measurement of temperature at depths varying from surface to 300 m and have proved very useful for the rapid location of thermoclines. Another model has been towed behind a ship, the output from the meter being fed to a strip chart recorder, thus enabling a continuous record of temperature to be obtained. Work is proceeding on another model which will use a single woven steel conductor PVC covered cable, so allowing the temperature sensing head to go to a greater depth than is now possible with twin core VIR Cable, without serious streaming in the water when adverse weather conditions prevail. This unit will use the sea water as a return conductor.

Acknowledgements

The writer wishes to acknowledge the help received from Mr. W. Huggins in the many pressure tests, etc. and final mechanical drawings, from Mr. G. Baxter in the temperature tests and final calibrations, and from Mr. M. Howes in the wiring of the prototype models.

The help given by Mr. R. F. Russ of Solartron Ltd., and the kindness of the firm in giving technical information on their pressure transducer, is also gratefully acknowledged.

Summary

The paper describes new types of (i) a temperature-depth recorder and (ii) a thermistor thermometer.

The temperature-depth recorder draws an instantaneous profile on a graphed paper roll showing the relation between temperature and depth. The equipment comprises an underwater unit connected to a control unit and recorder through a 550 m length of cable. The thermistor thermometer is capable of reading temperature at some remote point by means of a thermistor temperature sensing unit joined through a length of cable to a control unit which has a micro-ammeter calibrated directly in °C.

Both equipments are accurate to $\pm 1\%$ full-scale deflection.

Primary Production in the High Venice Lagoon

By

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Introduction

The study of the primary production of organic matter both in fresh water and in the sea is one of the main purposes of hydrology (Gessner, 1944; Krey, 1953; Steemann Nielsen, 1954; Tonolli, 1952). In 1958–59 monthly measurements of the primary production of organic matter were made in High Venice Lagoon both at high and at low tide, following a modification of Steemann Nielsen's well known ^{14}C technique (Angot, Doty and Oguri, 1958; Jitts, 1957; Steemann Nielsen, 1952, 1958 a; Ryther, 1956 b; Ryther and Vaccaro, 1954).

Before examining the results, the hydrographic conditions of the Venice Lagoon may be considered in the light of recent investigations (D'Ancona, Faganelli, and Ranzoli, 1951; Vatova, 1958 a, 1958 b, 1960 a, 1960 b). At high tide, water of relatively high salinity and poor in nutrient salts enters the lagoon through the three canal gateways (see Fig. 1); at low tide the water returns to the open sea in somewhat altered conditions. It is less saline, contaminated, and full of nutrient salts originating from complex enzymatic bacterial, oxydative, and reductive processes, from the decay and partial successive mineralization of the drainage liquids and organic matter of all kinds coming from Venice with its 173,000 inhabitants and some surrounding islands as Murano, Burano, Torcello, Lido, etc.

The hydrographic conditions of the High Lagoon, and particularly the concentration of nutrient salts, undergo constant changes as they depend on the great and unceasing phenomenon of the incoming and outgoing tidal currents which are strong and rapid during the maximum tidal phase or on exceptional tides. Sea water enters the High Venice Lagoon through the canal gateway of the Lido. During the spring tides $154{\cdot}2 \times 10^6$ m^3 of sea water comes in and the lagoon then holds a total of $335{\cdot}4 \times 10^6$ m^3 of water. On neap tides the incoming water amounts to $34{\cdot}6 \times 10^6$ m^3, and the lagoon holds $77{\cdot}1 \times 10^6$ m^3. The outflow is greater on account of the 660×10^6 m^3 or so of fresh water that flows into the lagoon every year.

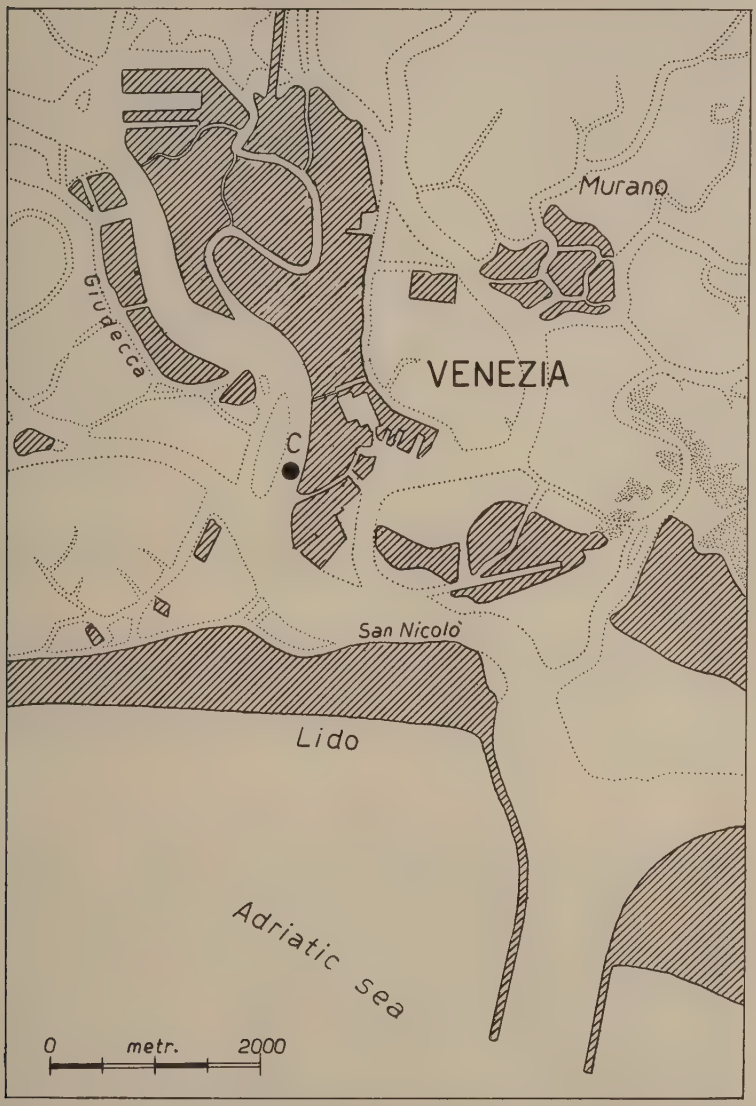

Figure 1. A chart of High Venice Lagoon showing the position of Station C at the Giardini buoy.

While a seasonal rhythm in temperature, salinity, and oxygen content can be noted both at high and at low tide, this is not noticeable in the concentration of nutritive salts because their inflow is constant. The temperature is subject to sharper oscillations than in the open sea (average temperature 6°–25°C), and the salinity is affected by the water of the rivers flowing into the North Adriatic at high tide, and by the fresh water discharged into the lagoon at low tide (average salinity 32–34·9‰). The lagoon water, which is not very deep and in constant motion, is always oversaturated with oxygen (101–105%) with the exception of the canals inside the city which have a low oxygen content.

The concentration of organic phosphorus in the lagoon is very low when the tide is coming in (1–2 mg/m^3) reaching 1–4 mg and sometimes even 17 mg/m^3 when the tide is receding. In the inner canals the phosphorus content reaches 137–288 mg/m^3, mainly due to human metabolites.

The water of the lagoon is very rich in ammonium nitrogen (NH_4), the concentration of which varies between 12 to 29 mg/m^3 at high tide and 18 to 112 mg/m^3 at low tide; in the city canals where the water is full of decaying organic matter the ammonium nitrogen content reaches considerable values (377–1,069 mg/m^3).

Nitrites are always present, their concentration being 3–7 mg/m^3 at high tide and 4–25 mg/m^3 at low tide. In the city canals the concentration is in the region of 35–37 mg/m^3 in spite of the presence of high quantities of ammonia. Nitrates vary from 33 to 37 mg/m^3 at high tide and from 52 to 71 mg/m^3 at low tide. A relation between the concentration of nitrate and oxygen content is shown by the fact that maximum concentrations occur in the cold months (94–105 mg/m^3), while in summer concentrations average 5–25 mg/m^3, coinciding with the minimum oxygen values.

Silicates are present in variable concentrations which are related at high tide with river discharges and at low tide with the fresh waters that flow into the lagoon. The average concentrations are 214–440 mg/m^3 and 742–753 mg/m^3 in the city canals on account of the greater inflow of fresh water which is very rich in silicates.

Methods

The transparency of the lagoon waters is generally rather low (VERCELLI, 1950), increasing when new water flows in and decreasing when bad weather stirs up the bottom or when violent rain carries muddy water into the lagoon which takes on a brown-yellowish colour. The transparency measured at the Giardini buoy (St. C in Fig. 1) with Secchi discs is generally higher at high tide. In 1958–59 the average transparency was 1·4 m at low tide and 1·9 m at high tide. Consequently the photosynthetic zone (calculated by multiplying the transparency value by a factor 3·3) varies from 4·6 m to 6·3 m respectively.

In order to determine primary production water samples were drawn directly from the surface near the Giardini buoy (St. C), generally twice a month both at high tide and at low tide. Four 125 ml Jena glass bottles were filled with this water to which 1 ml of $NaH^{14}CO_3$ solution was added. Three bottles were sunk into the water and left there for two hours, at depths of 0·2, 1·0, and 2·0 m respectively, while the fourth bottle was kept in the dark for comparison. This is of importance when the water is contaminated and full of bacteria (STEEMANN NIELSEN, 1960 a). No samples were drawn from greater

depths on account of both the limited extent of the photosynthetic zone and of the almost continual mixing of the water due to the tidal currents which prevent the stratification of plankton. Moreover, when the direction of the water flow is subject to continuous changes, the density and composition of the plankton population vary continuously.

The average production below unit surface is computed by multiplying the maximum rate found per volume with the depth of the photic zone and dividing by 2.

Results

According to the data collected at the Giardini buoy, the daily rate of primary production in the lagoon (see Table 1 and Figure 2, which represent the monthly production in g C/m²) increases rapidly from March (276 mg C/m²) to August (990 mg C/m²) when the surface temperature reaches its maximum values of 24·4 to 25·3°C at high tide and 24·6° to 25·7°C at low tide. In September the production decreases rapidly to 369 mg C/m², dropping to 17–133 mg C/m² in November–February, when the water temperature is 9·1°–7·3°C at high tide and 6·9°–5·4°C at low tide. In severe winters these values may fall to 1·8° and 0°C respectively.

Table 1

Organic production of water in the High Venice lagoon (Station at the Giardini buoy)

Date	Photosynthetic layer (m)		Duration of the photosynthesis (hours)	Production in mg C/m³		
	High tide	Low tide		High tide day	Low tide day	Total for the day
1958						
4. Aug.	5·1	3·0	14·2	223	687	910
13. Sept.	6·3	5·5	12·0	78	137	215
1. Oct.	4·9	6·8	11·4	28	57	85
11. Nov.	6·9	3·3	10·0	47	4	51
24. Nov.	6·7	4·1	9·0	21	8	29
1959						
30. Jan.	6·8	6·3	10·0	66	80	146
9. Feb.	6·8	4·4	10·0	27	23	50
25. Feb.	6.0	4,3	10.6	98	118	216
9. March	3·2	3·5	11·6	53	298	351
24. March	8·3	4·8	12·2	44	157	201
11. Apr.	4·0	3·4	13·2	89	332	421
24. Apr.	4·5	3·0	13·8	101	528	629
11. May	5·4	5·3	14·6	112	530	642
25. May	7·7	5·3	15·2	136	447	583
9. June	10·4	6·6	15·6	235	456	691
23. June	10·2	5·4	15·8	273	593	866
7. Aug.	11·3	4·9	14·2	313	1074	1387
22.–24. Aug.	10·8	7·1	13·8	234	360	594
15. Sept.	9·4	5·4	12·6	255	272	527
30. Sept.	3·0	4·1	11·6	53	158	211
16. Oct.	8·5	4·2	11·0	140	42	182
30. Oct.	1·6	2·2	11·0	12	–	–
30. Nov.	3·0	3·0	9·0	25	4	29
15. Dec.	3·4	2·7	8·6	10	5	15
22. Dec.	4·5	3·0	8·6	14	4	18

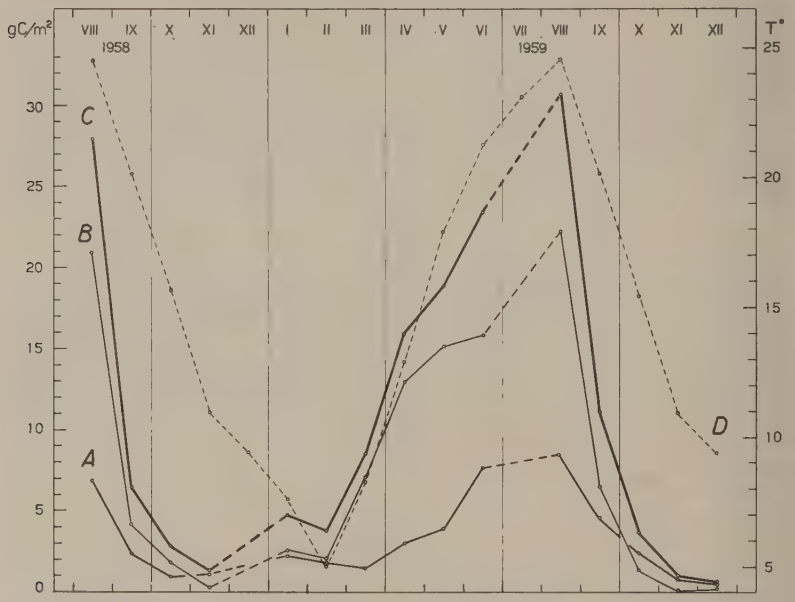

Figure 2. Monthly primary production (g C/m²) in High Venice Lagoon. (A) High tide. (B) Low tide. (C) Total production. (D) Average water temperature (1954—56).

The chief factors influencing the total daily production (high tide and low tide) therefore seem to be the temperature of the water, the duration of the assimilation which is about 10 hours in winter and 12–16 hours in spring and summer, light intensity, and the transparency of the water (RYTHER, 1956 a; STEEMANN NIELSEN, 1958 c; VOLLENWEIDER, 1956). But if we examine primary production at high and at low tide separately it is evident that from March to October production is higher at low tide than at high tide, in spite of the greater extent of the photosynthetic zone at high tide. For example, in the first 10 days of May 1959, while the photosynthetic zones have almost the same extent at high and low tide (5·4 and 5·3 m), primary production is 112 mg C/m² at high tide and 530 mg C/m² at low tide, that is almost five times greater. From the beginning of March to the end of August the total production is 29 g C/m² at high tide and 88 g C/m² at low tide, that is three times greater (maximum August values 313 and 1074 mg C/m² per day respectively). In spring and summer production is highly affected by the supply of nutrient salts, particularly of phosphates and nitrates originating from Venice and its environments. It should be added that, according to MARCHESONI (1954) and RANZOLI (1954), the amount of outgoing plankton is always smaller than the amount of incoming plankton, but the latter undergo an almost complete destruction as it proceeds from the open sea to the lagoon and consequently primary production is lower at high tide.

In the cold months, however, from September to February, the total production at low tide seems to be almost the same as at high tide, i.e. 14 and 13 g

C/m² respectively. But it should be noted that lagoon waters are more readily affected by the changes in the air temperature than the open sea, and in cold months (November–March) the water flowing in is warmer than the water flowing out, whereas in hot months (April–October) the reverse is the case.

The maximum rate of production at high tide occurs mostly at a depth of 1 to 2 m, almost never at the surface; at low tide, on the contrary, it takes place at the surface, seldom at 1 m and never at 2 m depth. Consequently, the maximum rate of production is related to the transparency of the lagoon waters.

Discussion

In the High Venice Lagoon, whose waters are rich in nutritive salts, the primary production for the year 1959 appears to be 42 g C/m² at high tide and 105 g C/m² at low tide, the total yearly production being 147 g C/m². If it is compared with the production in other seas (see Table 2), we shall see that, according to STEEMANN NIELSEN (1958 b), the yearly production is 39–175 g C/m² in the Danish waters (Sound and Isefjord) and 29–98 g C/m² in the Greenland coastal waters. During his cruises on the "Galathea", STEEMANN NIELSEN found that the daily production in the Pacific Ocean between California and New Zealand was 0·10–0·19 g C/m², while it was 0·14–0·19 g C/m² between Panama and the Channel (Atlantic Ocean); 0·056–0·075 g C/m² in the Antilles Current and 0·043–0·058 in the Sargasso Sea. The highest rate, 3·8 g C/m² per day, was measured in Walvis Bay at the Atlantic coast of South Africa (STEEMANN NIELSEN and AABYE JENSEN, 1957).

The average production for all oceans is about 0·15–0·19 g C/m² per day, that is 55–70 g C/m² per year and the total net production is estimated at $1{\cdot}2 - 1{\cdot}5 \times 10^{10}$ tons carbon per year (STEEMANN NIELSEN, 1960 b).

Passing on to fresh water, we shall find that yearly production is 30 g C/m² in the Lunzer Untersee in Austria (STEEMANN NIELSEN, 1959), about 200 g C/m² in Lake Furesøen in Denmark (STEEMANN NIELSEN, 1958 d) which is a eutrophic lake, and 104 g C/m² in Lake of Erken in Sweden (RODHE, 1958).

Table 2

Production of organic matter in different bodies of marine and fresh water

Water body	Gross production g C/m² per year	Author
High Venice Lagoon	147 (1959)	this paper
Danish water	39–175 (1953–56)	STEEMANN NIELSEN (1958 b)
Greenland coastal waters	29–98 (1954)	STEEMANN NIELSEN (1958 b)
Pacific	37–70 (1950–52)	STEEMANN NIELSEN and AABYE JENSEN (1957)
Atlantic	51–70 (1950–52)	STEEMANN NIELSEN and AABYE JENSEN (1957)
Sargasso Sea	18 (1950–52)	STEEMANN NIELSEN and AABYE JENSEN (1957)
Antilles Current	20–28 (1950–52)	STEEMANN NIELSEN and AABYE JENSEN (1957)
Lunzer Untersee (Austria)	30 (1953–54)	STEEMANN NIELSEN (1959)
Lake Furesøen (Denmark)	200 (1950–54)	STEEMANN NIELSEN (1958 d)
Lake Erken (Sweden)	104 (1953–56)	RODHE (1958)

From these preliminary investigations it is evident that on account of the considerable population of Venice and its environments that provide an inexhaustible mine of nutritive salts, primary production in the High Venice Lagoon is higher than in most other marine areas, being rather akin to the production in some eutrophic lakes in Europe.

Acknowledgements

Very special thanks are due to Prof. E. STEEMANN NIELSEN of the Royal Danish School of Pharmacy of the University of Copenhagen whose assistance and suggestions made these investigations possible.

Summary

1. The primary production of organic matter in the High Venice Lagoon or Lido basin was determined through the ^{14}C technique. The extent of the photosynthetic zone was calculated by multiplying the transparency, measured with Secchi discs, by 3·3.

2. In the spring and summer of 1959 the production at low tide was about three times greater than the production at high tide, values being 88 and 29 g C/m^2 respectively, notwithstanding the smaller extent of the photosynthetic zone (4·6 m at low tide and 6·3 m at high tide). The difference is due to the presence of nutrient salts, particularly phosphates and nitrates, which originate from the decay of the drainage liquids coming from Venice and its environments.

3. In the autumn and winter of 1959, however, the production at low tide was almost the same as at high tide, values being 14 and 13 g C/m^2 respectively, owing to the lower temperature of the water at low tide.

4. In 1959 the average yearly production in the High Venice Lagoon, which is a eutrophic lagoon, was therefore higher than in most marine areas, its values being 42 g C/m^2 at high tide and 105 g C/m^2 at low tide (total yearly production 147 g C/m^2). The total net production is estimated at $1{\cdot}2 \times 10^4$ tons carbon per year.

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The Seasonal Cycle of the Plankton in the North Sea and the North-Eastern Atlantic

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Introduction

The purpose of this paper is to describe some aspects of seasonal cycles in the plankton of the waters round the British Isles, using measures of "Total Phytoplankton" and "Total Copepods" to illustrate the distributions.

The data were derived from the results of the sampling carried out during the years 1948 to 1956 as part of a long-term survey of the plankton in the North Sea and the north-eastern Atlantic using the Continuous Plankton Recorder. This survey, which began in 1931 at the University College of Hull, is now conducted from the Edinburgh Oceanographic Laboratory.

Methods

The Recorders are towed by merchant ships and Ocean Weather Ships, at monthly intervals whenever possible, along a number of standard routes (see Fig. 1). The details of the individual tows during the period 1948 to 1956 are given by RAE (1952, 1953, and 1955) and by JOHN and BROWN (1958).

The Continuous Plankton Recorder (HARDY, 1939) is towed at a depth of about 10 m and it samples the water through an aperture of $\frac{1}{2}$ in. square. The plankton is filtered through a slowly moving band of bolting silk which has 60 meshes to the inch. The plankton is held in place by a second band of silk and the double band is wound on to a storage spool in a tank containing formaldehyde. When the Recorder is returned to the laboratory the roll of silk is unwound and divided into a number of sections, each representing 10 miles of tow. As a first step in the routine analysis of the Records, the intensity of any green or green-brown colour in each section of the bolting silk is estimated by eye by comparison with a standard colour scale; the results are assessed as "very pale green", "pale green", "green", and "very green". In order to give numerical values to these colour categories, acetone extracts of a small number

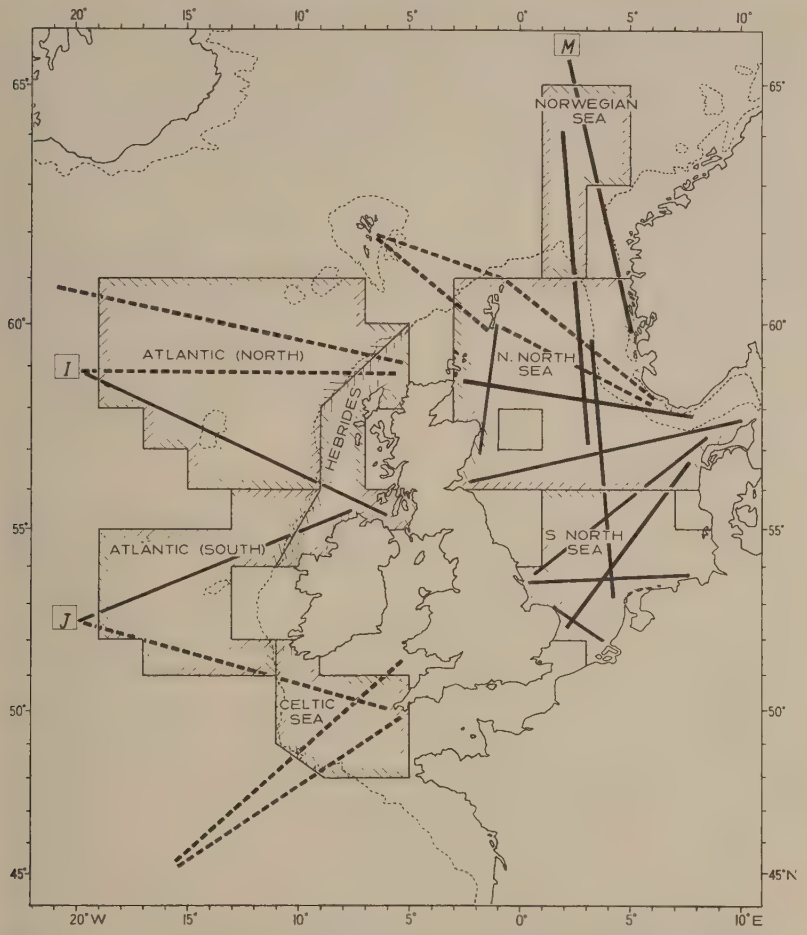

Figure 1. A chart showing; the approximate routes along which Continuous Plankton Recorders were towed during the period 1948–1956 (broken lines indicate alternative routes); the areas for which the seasonal cycles of the plankton are illustrated in Figures 2 a and b; the location of Ocean Weather Stations "I", "J", and "M".

of samples in each category were taken. These were compared by diluting the extracts until the colour of each was judged by eye to be of similar intensity to that of the weakest extract in the "very pale green" category. The volumes used for dilution were then used to calculate the relative strengths of the extracts. Corrected to an arbitrary scale, the "very pale green" samples varied between 0·6 and 1·5, the "pale green" between 1·4 and 2·8, and the "green" between 4·5 and 9·6. "Very green" samples occurred infrequently in the

Recorder collections and as there were not enough of them in the test material to give a reliable average estimate of their colour intensity they have been included with the "green" samples.

The average values gave the ratios of "very pale green" to "pale green" to "green" as 1 to 2 to 6·5, and these values were used in the calculations of seasonal fluctuations which follow. This estimate gives a crude but nevertheless useful estimate of "Total Phytoplankton" although it is clearly subject to the inherent limitation of colour analysis arising from seasonal changes in the pigmentation of the phytoplankton.

Rae (1952) and Colebrook (1960) have described the routine analysis of Recorder samples. Each 10-mile section is traversed, using a microscope, to examine a sub-sample of 1/40 of the area of silk. The copepods in this sub-sample are identified and counted, providing an estimate of the species present in approximately 0·075 cubic metres of sea water. The measure of "Total Copepods" used here was obtained by summation of the counts of *Calanus finmarchicus*, *Centropages typicus*, *Acartia* spp., *Temora longicornis*, *Centropages hamatus*, *Pseudocalanus elongatus*, and *Paracalanus parvus*. The remaining species of copepods found in the samples were not sufficiently abundant to contribute significantly to the total numbers.

Using 60-mesh bolting silk, it would clearly be unwise to attempt a quantitative estimate of the total standing crop of phytoplankton and zooplankton. For example, only a small proportion of the diatoms is likely to be retained by silk with holes measuring 230 250 μ[1]). For these reasons "Total Copepods" have been used as representing the most important component of the zooplankton and no attempt has been made to introduce a comparable measure of other zooplankton groups. The euphausiids are probably the most serious omission, occurring frequently in numbers of the order of 10–30 per m^3 in Recorder collections.

It must be stressed, therefore, that the objective is to compare the estimates of phytoplankton and copepods taken with the Continuous Plankton Recorder. In spite of the limitations of sampling with 60-mesh silk, the Recorder survey is likely to show more clearly than any other existing technique, the nature of the month-by-month fluctuations in the plankton simultaneously over a wide area.

For the purposes of plotting results, the area covered by the Continuous Plankton Recorder survey has been divided into rectangles, each 1° Lat. by 2° Long. Averages of colour intensity and of total copepods in each of the rectangles in each month were calculated, combining all the data for the years 1948 to 1956. In order to illustrate the seasonal distribution of colour intensity and total copepods, the area of the survey was divided into a number of larger areas (see Fig. 1) and the averages of colour intensity and of total copepods were calculated by summation of the means in the 1° by 2° rectangles in each area in each month, and dividing the sums by the number of sampled rectangles. The areas shown in Figure 1 were selected with the intention of illustrating any variation in the seasonal distributions which might exist; they are similar to the areas used in the routine examination of Recorder material (which are designed to facilitate comparison with fishery statistics).

[1]) Lucas (1940, 1941, and 1942) and Robinson (1961) have listed the wide variety of diatom and dinoflagellate species which appear in Continuous Plankton Recorder collections.

It was anticipated that there might be variation with latitude and with the depth of the water. The Atlantic was, therefore, divided into four areas; two deep water areas lying beyond the continental shelf (indicated by the 100 fathom depth contour in Fig. 1) and two coastal areas, one north and one south of Ireland. The North Sea was divided into a northern and a southern area.

This choice of areas makes it possible to compare deep water and shallow water areas lying between the same latitudes, and three deep water areas lying between different latitudes.

Figures 2 a and b show graphs of the monthly averages of total copepods and colour intensity at a depth of 10 m in the areas given in Figure 1; it should be emphasized that the point for each month represents the mean value for all the sampling in that month during the nine years 1948–1956. The scale of the graphs of total copepods was related to the colour intensity scale by equating the ordinate of the mean of all the averages of total copepods to that of the mean of all the averages of colour intensity.

Results

Figure 2 a shows the seasonal cycles of phytoplankton and total copepods in four areas in which the depth of the water was less than 100 fms (see Fig. 1). During the first five months of the year, the seasonal cycles in the four areas were very similar. All the areas showed increases in the intensity of phytoplankton colour in March followed by maxima in April and more or less sharp decreases in May. There were corresponding increases in the numbers of copepods in March and April followed by maxima in May in all the areas except the southern North Sea where the maximum occurred in June.

From June until the end of the year the seasonal cycles of phytoplankton colour in the four areas were very different from one another. In the southern North Sea the phytoplankton maximum in April was followed by other peaks of about the same height in June, August, and October, after which the colour intensity decreased to the winter minimum. In the northern North Sea the colour intensity decreased to a minimum in June and increased again fairly slowly to give a second maximum in October. In the coastal Atlantic areas (Hebrides and Celtic Sea) the colour intensities remained at fairly low levels, except for a small peak in August in the Hebrides area.

There were less striking differences between the graphs for total copepods in the different areas, following the spring maximum. In all except the Hebrides area the numbers of copepods decreased fairly steadily to reach the winter minimum in January or February; there was, however, a small peak in September in the northern North Sea. In the Hebrides area the numbers of copepods remained high until October with peaks in July and September.

Figure 2 b shows the seasonal cycle in three areas in which the depth of the water was considerably greater than 100 fms. The seasonal cycles in these areas were very different from those illustrated in Figure 2 a. In both the Atlantic (north) and Atlantic (south) areas the phytoplankton increased in April, about one month later than in the shallow water areas, to give peaks in May or June; following this the colour intensities decreased slowly, the decreases being interrupted by very small peaks in October. The numbers of copepods in the Atlantic (north) and Atlantic (south) areas increased rapidly in May, again

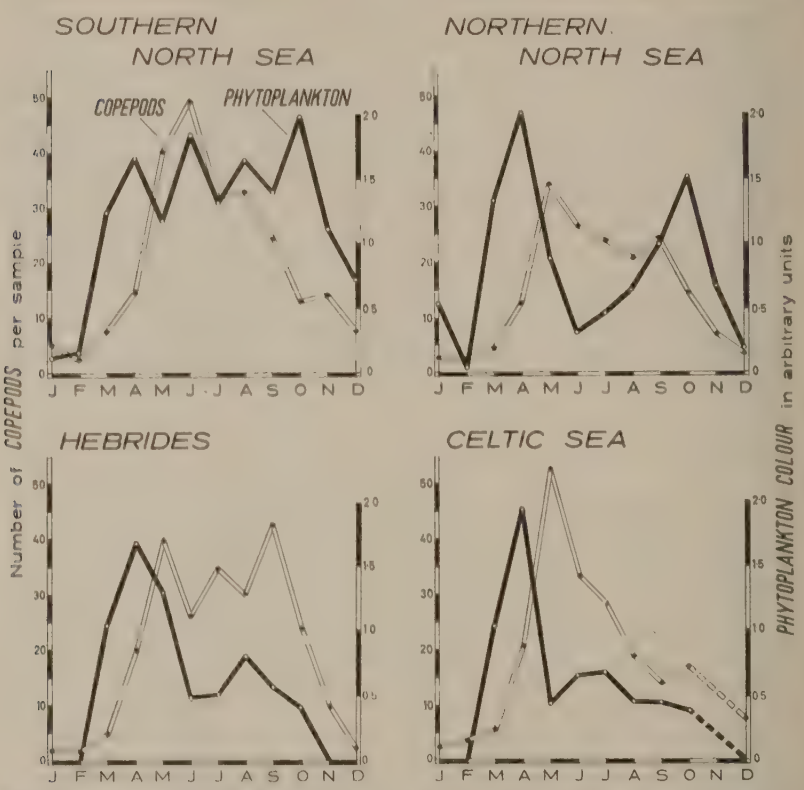

Figure 2 a. Graphs showing the seasonal variations (at a depth of 10 m) of the abundance of copepods and the amount of green (phytoplankton) colour on the Continuous Plankton Recorder silks in four areas with depths of less than 100 fms. Because of the duty rota of Ocean Weather Ships, there was no sampling in the Celtic Sea in November. Open lines show the fluctuations in the abundance of copepods and black lines of phytoplankton colour. The graphs were obtained by combining the results collected during the nine years 1948–1956. See Figure 1 for the location of the areas.

about one month later than in the shallow water areas, to give small peaks in May and much larger peaks in August to September.

The seasonal cycle in the Norwegian Sea differed from all the other areas in the relatively slow initial increase of the phytoplankton giving a small peak in May. This was followed by a rapid increase in July to give a much larger peak in July to August and a smaller peak in October. This cycle was very similar to the one described by HALLDAL (1953) based on material from Weather Station "M", which is situated just beyond the northern boundary of the Norwegian Sea area (see Fig. 1). HALLDAL ascribed the peaks in April and May to the increase in the amount of sunlight and the larger standing crop in July to the onset of stratification. The smaller peak in October was thought to be caused by the release of nutrients due to the breakdown of the thermocline.

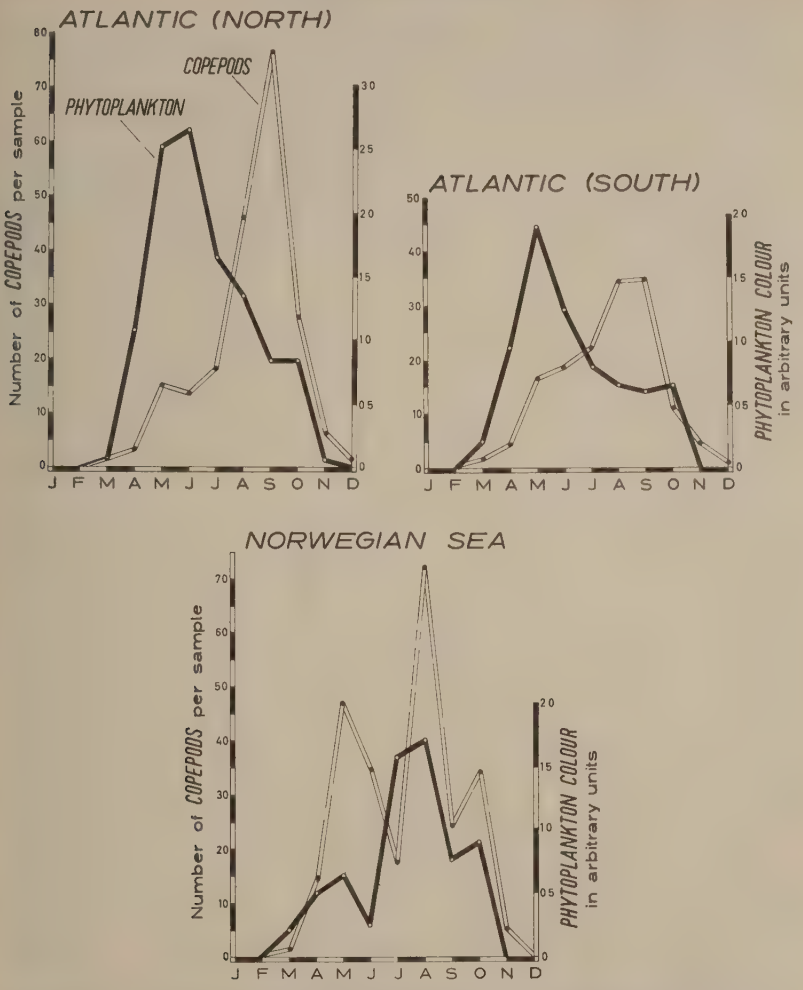

Figure 2 b. Seasonal variations of the copepods and phytoplankton in four areas with depths greater than 100 fms. For details see legends to Figures 1 and 2 a.

In the Norwegian Sea, the spring increase in the number of copepods occurred almost simultaneously with that of the phytoplankton, whereas in all the other areas the copepod increase occurred about one month later. Peaks in the numbers of copepods occurred in May, August, and October, in the same months as the phytoplankton peaks. ØSTVEDT (1955) studied the seasonal cycle of the copepods at Weather Station "M". His figure of the seasonal variations of total copepods in the surface layers shows peaks in the same months as

in Figure 2 b, but the relative heights of the peaks are rather different. In Østvedt's figure the peak in May to June is considerably higher than that in August and October.

Discussion

It is evident from Figures 2 a and b that there were considerable differences in the form of the seasonal cycle in the various areas shown in Figure 1. A cycle similar to the "classical" seasonal cycle of the plankton in temperate waters (see, for example, Russell and Yonge, 1928; Harvey, Cooper, Lebour, and Russell, 1935; Bogorov, 1958) was in fact found only in the northern North Sea.

There appear to be two main reasons for these differences; first, variations in the physical factors which affect the plankton as a whole, and second, variation in the composition of the plankton, which is related to the different geographical distributions of the species which make up the plankton. These two sources of variation are not necessarily interrelated: the geographical distribution of a species may be regulated, at least in part, by factors which are not normally considered to be important in determining the seasonal fluctuation of the abundance of the plankton as a whole.

The duration of the plankton season may be related in some way to the depth of the water. In the southern North Sea, which has an approximate average depth of 15 fms, the spring increase of phytoplankton occurred in March and the decrease to the winter minimum was not complete until the following January. In the northern North Sea and the two coastal Atlantic areas, which had average depths in the order of 50 fms, the spring increase took place at the same time as in the southern North Sea but the decrease to the winter minimum was complete between one and two months earlier. The average depth of the three deep water areas in the Atlantic and the Norwegian Sea was of the order of 500 fms, and in these areas the spring increase of phytoplankton did not take place until April, about one month later than in the shallow water areas. On the other hand, the decrease to the winter minimum occurred at about the same time as in the northern North Sea and the coastal Atlantic areas.

In the shallow waters of the southern North Sea it seems likely that vertical mixing of the surface and bottom waters can occur fairly easily, thus facilitating the replenishment of nutrients in the surface water. In the remaining areas the greater depth of the water may have precluded any extensive replenishment of nutrients with the result that the abundance of the phytoplankton decreased to the winter levels earlier than in the southern North Sea.

It is fairly well established that two factors determine the timing of the spring increase of phytoplankton, assuming that there is a sufficient supply of nutrients; first, the increase in the amount of sunlight, and second the vertical stability of the water (see, for example, Riley, 1942; Sverdrup, 1953; Marshall, 1958; and Cushing, 1959). Two pairs of areas (southern North Sea and Atlantic, south: northern North Sea and Atlantic, north) lay between similar latitudes and each pair presumably received approximately the same amounts of sunlight. Therefore, unless the Atlantic water was much more turbid than the North Sea water, which is most unlikely, the amount of sunlight received could not have caused the differences in the timing of the spring increases in these areas.

There appear to be few published data on which to base a comparison of the vertical stability in the North Sea and the Atlantic, but it seems reasonable to suppose that there is a difference in the timing of the establishment of a sufficient degree of vertical stability in the shallow waters of the North Sea and the deep waters of the Atlantic, and that this may cause differences in the timing of the spring increases of the phytoplankton.

CORLETT (1953) described the seasonal cycles of the abundance of diatoms and dinoflagellates at Weather Stations "I" and "J" for the years 1948–1950. These stations lie just beyond the western boundaries of the Atlantic (north) and Atlantic (south) areas respectively (see Fig. 1). CORLETT showed that, in two years out of the three which were studied, the spring increase of diatoms occurred earlier at the more southerly station "J" than at station "I". Similar differences in the timing of the spring increase were not shown in the Recorder samples. CORLETT demonstrated two separate spring and autumn maxima, particularly at station "I". The figures presented by CORLETT and those in Figure 2 b are difficult to compare because they are based on different sampling techniques and methods of analysis, and different scales have been used to present the illustrations. CORLETT separated diatoms and dinoflagellates in his figures, and the graphs in Figure 2 b suffer from the smoothing effects of averaging nine years' data. Nevertheless, with the exception of the differences noted above, the general features of the seasonal cycle of the phytoplankton demonstrated by the two methods are similar; for example CORLETT's material, like the Recorder results, showed that the standing crop in the autumn was much smaller than that in the spring.

The variations in the seasonal duration of the copepods (in Recorder samples) corresponded with those of the phytoplankton with the exception of the timing of the spring increase in the Norwegian Sea. The correspondence is probably due to the grazing relationship between phytoplankton and copepods (see, for example, CUSHING, 1959).

An ideal plankton community might contain a sufficient number of abundant species, both of phytoplankton and zooplankton, to provide a continuous succession of dominant species or groups of species which would be capable of utilizing most of the available nutrients. There were several clear examples of departures from this ideal in the plankton cycles illustrated in Figures 2 a and b.

In both the deep water Atlantic areas the numbers of copepods in the spring were low relative to the abundance of phytoplankton when compared with the balance in the other areas. It is difficult to suggest an explanation of this difference but one possibility lies in the specific composition of the copepods in the spring which, in the other areas consisted chiefly of *Calanus finmarchicus* and the group *Pseudocalanus* spp. and *Paracalanus* spp. These species, however, did not occur very abundantly over the deep water in the Atlantic (COLEBROOK, JOHN, and BROWN, 1960) and it would appear that there was no other copepod which could take the place of these abundant species.

The heights of the August–September–October peaks in the numbers of copepods in all the Atlantic areas and in the Norwegian Sea were determined almost entirely by the abundance of *Acartia* spp. It occurred fairly abundantly inside the continental shelf in the Hebrides area but in smaller numbers in the Celtic Sea area; it was also more abundant in the Atlantic (north) area than in the Atlantic (south) area. These variations are reflected in the respective graphs of total copepods.

Sømme (1934) and Wiborg (1958) have shown that a considerable population of *Calanus finmarchicus* overwinters in deep water in the Norwegian Sea and that this population migrates upwards into the photic zone in the early spring. The peak in the numbers of copepods in April, May, and June (Fig. 2 a) consisted almost entirely of the Vth and VIth stages of *Calanus finmarchicus*, thus producing a very different balance between copepods and phytoplankton than that found in the other areas.

In the type of mathematical model of the seasonal cycle of plankton which has been put forward by Riley, Stommel, and Bumpus (1949), Cushing (1959), and others, it has been assumed that the plankton community approximated to the ideal form in which there is a continuous succession of dominant species. In order to achieve a single model that could be applied to all the seasonal cycles shown in Figures 2 a and b it would be necessary to introduce separate terms describing the dynamics of at least some of the more important individual species.

Summary

1. The Continuous Plankton Recorder survey of the North Sea and the north-east Atlantic is used to provide estimates of "Total Phytoplankton" (based on estimates, by eye, of the intensity of the colour of the Recorder silks) and "Total Copepods" (a summation of the counts of the common species). Figures 2 a and b, a combination of all the data available from the years 1948 to 1956, illustrate the seasonal variation in the amount of phytoplankton colour and total copepods retained by bolting silk of 60 meshes to the inch, sampling horizontally at a depth of 10 m. The areas sampled are shown in Figure 1.

2. The plankton season was of longer duration over shallow water than it was over deep water. This was possibly caused by variation in (a) the timing of establishment of a sufficient degree of vertical stability to permit a marked increase in the abundance of phytoplankton and (b) the extent of the vertical mixing between surface and bottom water on which the replenishment of nutrients is dependent.

3. The presence and the absence of several peaks of abundance of total copepods could be attributed to one or a few species. This implies that, at least in some of the areas, there was a departure from the ideal of a continuous succession of dominant species covering the whole plankton season.

4. It is concluded that it would be difficult, without separate terms for the dynamics of the most important species, to derive a single mathematical model which could describe the seasonal cycles of the plankton in the different parts of the survey.

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The Effect of Salinity on the Survival and Distribution of Larval and Young Fish

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Introduction

Salinity is one of the most important factors which affects the survival and distribution of fish at different stages of their life. Many marine fish come near the estuaries to spawn so that the development of the eggs and early larval stages occur in water of low salinity. Other fishes like *Salmo salar* L. migrate to freshwater bodies to spawn and the development of the eggs and the young stages take place in fresh water before their seaward migration. The effect of salinity may be direct by affecting the survival of fish or indirect by affecting the amount of plankton which constitutes the main food of the early larval stages (JOHANSEN, 1927; WALFORD, 1946; KÄNDLER, 1950; and JENSEN, 1952). That the salinity affects the distribution of fish was found by many investigators (JOHANSEN, 1908; HENSCHEL, 1936; POULSEN, 1937; GUNTER, 1945; MANKOWSKI, 1948; BÜCKMANN, HARDER and HEMPEL, 1953; and HOURSTON, 1953).

A correlation between the salinity and the quantity of cod fry and larvae was found by POULSEN (1930) and KÄNDLER (1950). Recently it was found that there is a positive correlation between the salinity and the strength of year-classes (WALFORD, 1946; ALANDER, 1952, and JENSEN, 1952). WALFORD (1946) inferred that the increase in salinity was associated with wind (SVERDRUP, MARTIN, and FLEMING, 1942), and SVERDRUP (in WALFORD, 1946) confirms this finding. However, POULSEN (1931) did not find significant correlation between salinity and the strength of year-classes. Later (1944) he maintained that the strength of year-classes is affected by other factors (i.e. temperature and plankton).

The effect of salinity either on freshwater fish or on anadromous and catadromous fishes was studied by many investigators (BERT, 1871; RUTTER, 1904; SUMNER, 1960; FAGE, 1912; RAMULT, 1927; HUNTSMAN and HOAR, 1939; AUVERGNAT and SECONDAT, 1941; BUSNEL, 1943; BUSNEL, DRILHON and RAFFY, 1946; PYEFINCH, 1955; BLACK, 1957; HERBERT and MANN, 1958; PARRY, 1958, 1960; PARRY, HOLLIDAY, and BLAXTER, 1959 etc.).

Survival and the ability to osmoregulate in different salinities depends upon the size and age of fish (BERT, 1871; RUTTER, 1904; FAGE, 1912; ROBERTS and

Jee, 1923; Keys, 1931; Huntsman and Hoar 1939; Auvergnat and Secondat, 1941; Gunter, 1942; Black, 1951; Pyefinch, 1955 and Parry, 1958 and 1960), as well as on the species (Henschel, 1936; Parry, 1958 and 1960). Parry (1960) in her study of three salmonid species concluded that the size, rather than the age, appears to be the more important factor in their tolerance of higher salinities.

The degree of resistance of freshwater fish to different salinities can be increased by acclimation (Bert, 1871, 1873, 1883; Ramult, 1927; Chaisson, 1934, and Black, 1951). The fact that fish can discriminate between different salinities was shown by many investigators (Chidester, 1922; Bull, 1938; and Shepard 1948 (in Black, 1951). Chidester (1922) showed that although *Fundulus heteroclitus* can discriminate between different salinities, the effect of different temperatures or stream flow is more powerful.

The aim of the present investigation is to find out the effect of different salinities on the early larval stages of some marine and freshwater fish as well as their salinity tolerance during this critical stage of life. The results of this experimental study may help in explanation of the behaviour, distribution, survival, and osmoregulation of fish larvae at the very early stages just after hatching. In addition it may explain the ability of some larval fish to tolerate environmental changes and would provide information relevant to their distribution in nature.

Apparatus and Technique

Many fish larvae can live for a few hours to a few days at different salinities but if exposed to such salinities for longer periods they die. Thus in experiments on the study of the effect of different salinities on fish larvae long-term experiments should be carried out. Previous methods used in studying the effect of different salinities on fish and other marine animals were of two types. In the first method water of known salinity was prepared and renewed at regular intervals (Ramult, 1927; Parry, 1958 and 1960). In the second method a constant water flow of a definite salinity was passed over the experimental animals (Loosanoff and Smith, 1951). Reactions of fishes to salinity gradients were carried out by Doudoroff (1938) and Shepard (1948). In the present investigation the two methods were adopted but it was found necessary to use a continuous water circulation when experimenting with some marine fish larvae.

Apparatus providing constant water flows of known salinity

In this apparatus fresh and sea water were mixed in different ratios to give water of different salinities. The apparatus consists of two constant level tubes A and B (Fig. 1) of 5 cm (2″) diameter and 42·5 cm (17″) long. D and D′ are inlets for sea water and fresh water situated near the bottom of the tubes, while C and C′ are overflows to ensure a constant level of water in both tubes. A two-hole rubber stopper closes tube A at the bottom through which passes the two outflows E and F. These outflow tubes take water from near the middle of the tube A, an arrangement found necessary to ensure the use of as clean sea water as possible. Tubes G and H are outflows from tube B arranged in the same way as in A. Each of the outflows (E, F, G, H) is connected to a glass T-piece (Fig. 2). Thus a total of four outflow tubes can supply water from the main tubes A and B. Each of these is connected by rubber tubing to a glass

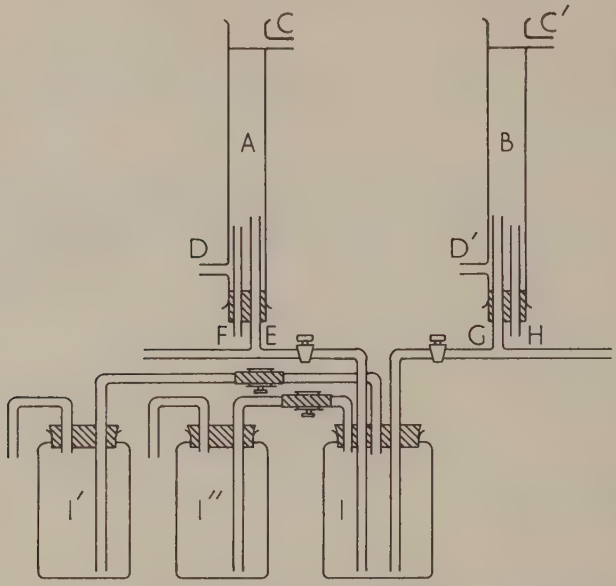

Figure 1. Apparatus for supplying a constant flow of water of different salinities.

tube provided with a stop-cock and continuing to the bottom of one of four mixing bottles (I, J, K, L). Each mixing bottle thus receives two tubes one with water from A, the other from B (one being salt the other fresh). By appropriate manipulation of the stop-cocks on the flow tubes any desired salinity can be obtained in the mixing bottles. In these bottles incoming water was thus carried to the bottom whilst the outflow was taken from the top. This arrangement was found to produce a thorough mixing of the fresh and sea water resulting in the supply of water of uniform salinity. The efficiency of this arrangement was tested by the introduction of coloured water either dyed or made turbid with milk (Bull, 1938) in one of the main tubes (A or B) which gave a uniform solution in the mixing bottles.

Water from each of the mixing bottles (I, J, K, L) supplies two experimental bottles each of 250 to 350 ml capacity, rubber tubing forming connection between them. As it was necessary to maintain a slow water flow, screw clips were fitted on this rubber tubing so enabling any desired flow to be obtained. A slow flow was found important in experimenting with larval fish so as to avoid washing them through the overflow. To ensure thorough, complete renewal and circulation of water in the experimental bottles the inflow was taken from near the bottom, and the outflow from near the top. All outflows were provided with a nylon netting inside the bottles to prevent washing out of the larvae.

With this apparatus four constant different salinities can be obtained, and eight experiments carried out (two for each salinity) at the same time. The apparatus can be used not only for different salinities, but also combinations of different salinities with other factors can easily be carried out. Thus, to

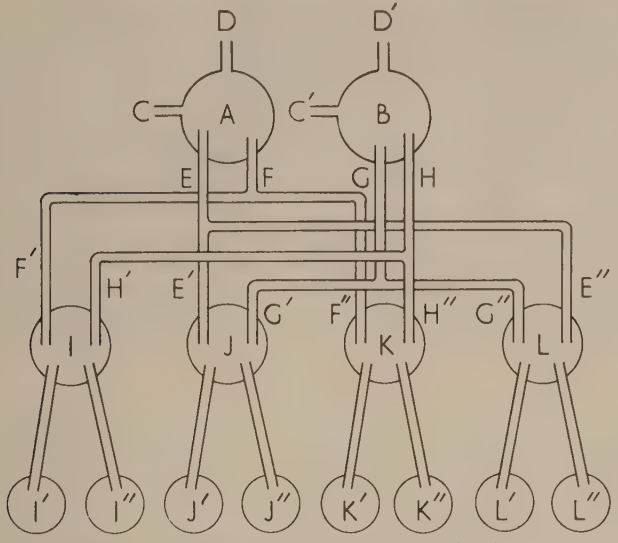

Figure 2. Top view of the apparatus shown in Figure 1.

study the effect of different salinities under different oxygen tensions, nitrogen can be bubbled through diffusers in the main tubes A and B. With the use of carbon dioxide, water of different salinities and low hydrogen ion concentrations could be obtained, although this was not actually done in the present investigation.

It should be mentioned that the use of stop-cocks presents many difficulties especially if the experiment is carried on for long periods (more than a week). It was noticed that the stop-cocks become blocked either by dirt or growth so that the salinity undergoes changes as time goes on. Dirt was eliminated by using sea water filtered through sand. In addition, as previously mentioned, the outflow of water from the main tubes A and B to the mixing bottles was taken from near the middle to give any dirt present the chance to settle to the bottom, and the inflow of water supplying the main tubes A and B was situated near the bottom. In spite of all these precautions, it was observed that some of the stop-cocks became partly blocked, especially when using very low salinities, so that cleaning of the tubes and stop-cocks had to be carried out frequently.

Experiments using Standing Water of Known Salinity

In addition to using a continuous water flow of a known salinity, experiments in standing water were also carried out. In the case of herring larvae, it was found difficult to keep the larvae in a bottle with a continuous water flow due to the extreme delicacy of the larvae, which having once touched the overflow, withered and eventually died. These larvae can, however, be kept for long periods (a week or even two weeks) in standing water without being harmed, so in experiments with herring larvae water of known salinity was used

without renewal until the end of the experiment. In all experiments controls were used. In the case of salmonid larvae (salmon, sea trout, and brown trout) water of known salinity was used and renewed every week, 15 alevins being kept per jar of three litres capacity. Water in these jars was occasionally aerated.

The salinity tolerance was measured by recording the times of the death of fish, thus the survival time could be considered in relation to salinity. The survival of fish is expressed in terms of the median survival time, i.e. the time at which 50% of the fish survived at certain salinity throughout the duration of the experiment. The experiments were carried out until all subjects died or no mortality took place for very long periods, i.e. 10 weeks.

The "chlorine" content of water was determined by MOHR's method in which titration was done with silver nitrate standardized against "Eau de mer normale" supplied by the Association d'Océanographie Physique, Denmark. Salinity was derived from KNUDSEN's Hydrographical Tables (1901).

Material

The fish larvae used in these experiments were herring (*Clupea harengus* L.), lump-sucker (*Cyclopterus lumpus* L.), salmon (*Salmo salar* L.), sea trout (*Salmo trutta*), and brown trout (*Salmo trutta* f. *fario*). Herring larvae were reared in the laboratory after artificial fertilization from fish collected from the North Sea. For salmonids the artificial fertilization was carried out at Rothbury Fish Hatchery, England, through the courtesy of the Northumberland and Tyneside River Board. In addition, artificial fertilization with brown trout was carried out at Welham Park Fish Hatchery, Malton, Yorkshire, England. Eggs of lump-sucker were collected from near the laboratory. The fish larvae were reared at the Dove Marine Laboratory, Cullercoats, North Shields, England. Rearing of the larvae took place either in glass or glazed earthenware tanks. The average lengths of the larvae used and the temperatures at which they were reared were as follows:—

Species	Temperature °C	Length of larvae mm	Age (days)
Clupea harengus L.	13·1–14·8	6·5– 9	1– 9
Cyclopterus lumpus L.	10·1–13·2	6–10	1–28
Salmo salar L.	7·9–12·5	20–25	1–42*)
Salmo trutta	5 –10·5	18–24	1–42*)
Salmo trutta f. *fario*	5 – 9·2	16–25	1–42*)

*) Yolk-sac absorbed 28–35 days after hatching.

Young plaice (*Pleuronectes platessa* L.) 38–50 mm long, collected from near the laboratory was also used. It was, however, difficult to obtain plaice larvae.

Experimental Results

1. Herring larvae

Four sets of experiments were carried out on newly hatched herring larvae, at salinities from 30·04 to 2·5‰. A control was carried out where the larvae were placed in ordinary sea water (salinity 33‰). All experiments were carried out in static water at 13–15°C. The results are represented in Figure 3 showing the relation between the median survival time and salinity. Results show that herring larvae live better and longer at salinities of 10‰ to 15‰. Thus while

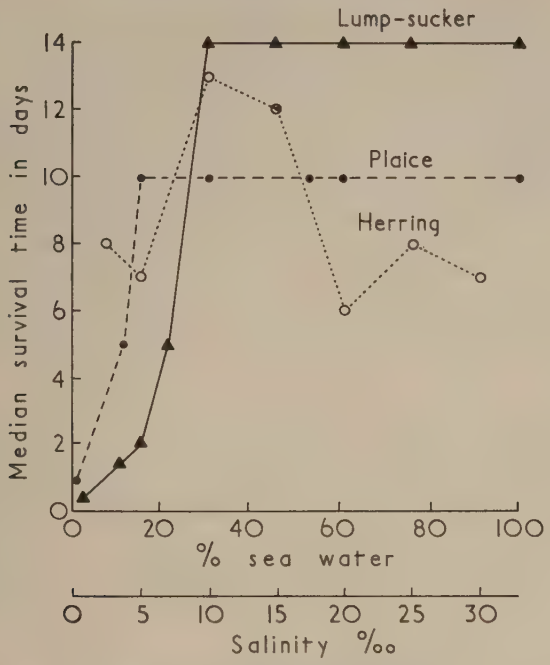

Figure 3. Relative survival time at different salinities of some larval and young marine teleosts.
○ ····· ○ = *Clupea harengus* L. larvae
▲——▲ = *Cyclopterus lumpus* L. larvae
● ------ ● = *Pleuronectes platessa* L. young

the larvae lived at 10‰ for 13 days, they lived for 12 days at 15‰, and 7 days at 5‰. In ordinary sea water (i.e. control experiment) the larvae lived for only 7 days. It seems, therefore, that salinities as low as 10‰ are favourable for the survival of herring larvae. They can live, however, at salinities of 2·5‰ but not in fresh water for shorter periods. It is concluded that low salinities are not harmful to herring larvae if prevailing for short periods only. In all experiments the mortality at the end of the experiment was due to starvation and not to lowered salinity. Attempts to feed the larvae with newly hatched *Artemia salina*, nauplii of *Tigriopus fulvus* F., phytoplankton, and the digestive gland of the shore crab (*Carcinus maenas*) were unsuccessful.

The pH range in the salinity experiments was favourable for the larvae, i.e. 7·8–8·15 (Bishai, 1960 b). The oxygen saturation was above the lethal level, i.e. 80% (lethal level below 50%, Bishai, 1960 a).

2. Lump-sucker larvae

All experiments were carried out in the salinity apparatus with running water using five or ten larvae in each experiment at 12·9 ± 0·5°C. A control was carried out under the same conditions of water circulation, temperature, and

feeding. The results are represented in Figure 3 which shows that lump-sucker larvae can live for at least 14 days at salinities as low as 9 ‰, at 5 ‰ the larvae lived for 48 hours. Any salinity below 5 ‰ proved to be fatal.

It was desirable to find out the effect of acclimation on the median survival time. Several experiments were carried out where larvae were acclimated for several days (4 days) to live at a salinity of 5·54 ‰. These larvae will die within 12 hours if the salinity was changed to 4·7 ‰. Acclimation may increase the median survival time for low salinities but not the lethal limit. Another experiment was carried out where gradual acclimation took place when 9 days old larvae, which were acclimated to live for 10 days at salinities from 8·86 to 7·52 ‰, were placed in water of 5·34 ‰. Mortality began and only one larva out of four lived for further 4 days.

The age of lump-sucker larvae (i.e. newly hatched to 21 days old) seems to have no effect on their survival at low salinities.

3. Young plaice

As larvae of plaice could not be obtained during the present investigation, young plaice (38–50 mm) was used. The results are shown in Figure 3 and show that young plaice can live for 10 days (at least) at salinities as low as 5 ‰. At lower salinities, i.e. 3–4·4 ‰, they can live for 5 days without any harmful effects. In fresh water young plaice can live for 20 hours. At salinities higher than 5 ‰ no mortality took place. The experiments were carried out at 16·8°C (±0·2), and at an oxygen saturation of 86 %. The pH values were within the favourable limits (i.e. 8·20–7·7, Bishai, 1960 b).

4. Salmon, sea trout, and brown trout alevins

Experiments were carried out in 3 litre jars in which the water was renewed. Five larvae of each species were used. As soon as the greater part of the yolk-sac was absorbed, the alevins were fed with the digestive gland of the shore crab *Carcinus maenas* as well as with *Daphnia* sp. The alevins were fed three times daily during the first month and twice daily during the second and third months. The results are represented in Figure 4 and show that the newly hatched alevins of the three species can live in a salinity range of 1·64 ‰ to 8·20 ‰ (5–25 % sea water) for at least ten weeks when the experiment was ended. At higher salinities salmon alevins were more resistant than sea trout and brown trout alevins, sea trout having the lowest resistance. Whilst the larvae were lively in salinities of 5 % sea water those at 30 % sea water were less active and developed slowly. The yolk-sac of such larvae appeared whitish on the outside. At higher salinities, i.e. 40 and 50 % sea water, salmon alevins are more resistant and can live for 18 days in 40 % sea water while brown trout and sea trout can live for 11 and 9 days respectively. At 50 % sea water all the alevins died within 11 days, salmon alevins being the most resistant living for 10 days while sea trout and brown trout lived for a week. Control experiments were carried out which showed that salmonid alevins lived for the duration of the experiment (i.e. 10 weeks) without any mortality.

If placed in sea water, salmon alevins live for 8 hours, while sea trout and brown trout live for $2\frac{1}{2}$ and $3\frac{1}{2}$ hours respectively, after which period they still recover when transferred to fresh water.

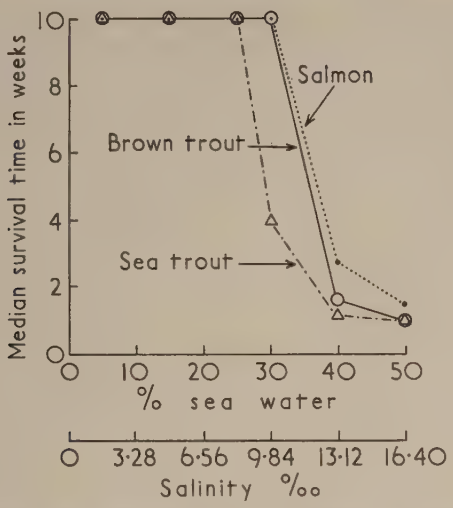

Figure 4. Relative survival time in sea water dilutions of salmonid alevins.
● ····· ● = *Salmo salar* L.
○———○ = *Salmo trutta* f. *fario*
△ -·-·-·- △ = *Salmo trutta* L.

Discussion

Many species of fish are exposed during their life to different salinities which may affect their survival and distribution either directly or indirectly. POULSEN (1937) found that the salinity changes in nature may be very great and sudden during the critical periods of development of fish. This author could not find a relation between the development of herring eggs and larvae and salinity changes owing to the lack of detailed investigations on these lines.

From the present investigation it is concluded that although herring larvae can live under experimental conditions for several days at salinities as low as 2·5‰, they live better and longer in 10‰ to 15‰. HOURSTON (1959) recorded the abundance of juvenile herring at salinities from 17·23 to 29·39‰ in Barkley Sound. Salinities below 10‰ may be unfavourable for herring larvae when prevailing for long periods (incubation and rearing of these larvae was done at 33‰ salinity). FORD (1929) found that herring larvae can live at salinities as low as 5‰ up to the time of yolk-sac absorption. The upper lethal limit of salinity for herring larvae was found by SCHACH (1939) to be 36‰. LEÖVEY (1938) attributed the injurious effect of salinities higher than that of sea water to the inability of chloride secreting cells to cope with the increased salinity.

Under experimental conditions young plaice (38–50 mm long) can live for at least 10 days at a salinity of 5‰. JOHANSEN (1908) in his field observations found that plaice may occur in water of salinities as low as 7–8‰. However, they did not occur in salinity lower than 5‰. HENSCHEL (1936) found that the flounder (*Pleuronectes flesus*) can survive in 4‰ chloride better than the plaice (*Pleuronectes platessa*). Such specific differences may be important in

the survival and distribution of these fish. After metamorphosis young plaice mostly move to inshore water and to near river estuaries and are thus subjected in nature to variation in salinity. If salinity below 5‰ prevails for long periods it may be lethal to such fish larvae as those of the lump-sucker, which cannot live for long periods at salinities below 7‰. Acclimation to low salinities may increase the median survival time but not the lethal limit. Lump-sucker larvae which were acclimated at 5·54‰ will die if subjected to lower salinities (i.e. 4·98‰ and 4·06‰). Larvae living at 33‰ will die within 48 hours when subjected to any salinity below 5‰. Thus it seems that there is a lower lethal limit of salinity which is not changed by acclimation.

Although low salinity may be favourable to pelagic fish larvae it is not so for the development of eggs (Johansen, 1908). This is attributed to the sinking of the eggs towards the bottom thus causing high mortality. During the early development of pelagic fish stages, high mortality associated with low salinities may be taking place during the egg development and not during the early larval stages. Johansen (1908) showed that whilst plaice eggs were unable to float at salinities below 10‰, the pelagic larvae may live in water of a far less salinity. In the present investigation results show that salinities as low as 4‰ do not affect the development of herring eggs which develop up to hatching in the same way as those in ordinary sea water (salinity 33‰). Outram (1951) concluded that in nature herring seems to favour spawning where freshwater influences are the greatest, and that fresh water or water of low salinity could be a stimulant which caused herring to spawn.

Low salinity, although it may be favourable for the survival of fish larvae, may not be suitable for the production of a rich plankton which forms the necessary food during the critical stage when the larvae begin to feed. High mortality of fish larvae associated with low salinity may be attributed to its effect on the food supply and not directly on the larvae themselves, as shown by Johansen (1927 a), Walford (1946), and Jensen (1952).

In case of freshwater fish the effect of salinity is usually a direct one. It was thought that the migration of catadromous fish is influenced by environmental factors including salinity, but it was recently shown that hormones may be active in initiating changes which doubtless cause fish migration (Fontaine, 1943, 1948, 1954; Fontaine *et al.*, 1948; Hoar, 1953). Nevertheless the effect of salinity on the survival of these fish remains important at times. In addition, the study of the salinity tolerance as well as the development of mechanisms for osmoregulation at different ages is of great importance in the ecology of the migratory fish. Anadromous fish may go directly to sea after hatching (Clemens and Wilby, 1946) or they may live for some time in either fresh or brackish water. Under experimental conditions newly hatched alevins of salmon, sea trout, and brown trout lived for at least ten weeks in 25 % sea water (8·20‰ salinity) without any mortality. At 30% sea water (9·84‰ salinity) while salmon and brown trout lived for ten weeks with low mortality (30%), sea trout lived for four weeks after which the mortality was high (60–80%). That salmonid alevins can live at salinities up to 30% sea water was found by many investigators (Fage, 1912; Ramult, 1927; Auvergnat and Secondat, 1941). At 40% sea water salmon alevins lived for 18 days while brown trout and sea trout lived for 11 and 9 days respectively. At 50% sea water salmon alevins lived without mortality for 10 days, while 80% of the sea trout and 50% of the brown trout lived for one week. It seems that 50% sea water is

injurious to salmonid alevins, thus confirming earlier findings (FAGE, 1912; RAMULT, 1927; AUVERGNAT and SECONDAT, 1941; BUSNEL, DRILHON, and RAFFY, 1946; PARRY, 1960). Salmon, sea trout, and brown trout alevins die if subjected to 100% sea water (33 $^0/_{00}$ salinity) for more than ten hours. It is concluded that salmon alevins are more resistant to salinity changes as compared to sea trout and brown trout alevins. The "salinity tolerance" of the alevins of the three species is as follows:—

S. salar L. > *S. trutta* f. *fario* > *S. trutta*

This result is interesting as the survival time of the brown trout which is a stenohaline freshwater fish is greater than that of the sea trout which is an anadromous fish. This finding does not agree with that found by HERBERT and MANN (1958) and PARRY (1960) who showed that stenohaline freshwater fish had the lowest survival time as compared with anadromous fishes. Comparing my results with those recently found by PARRY (1960) a marked difference is observed. Thus while the present work showed that newly hatched *Salmo salar* L. alevins lived for 10 weeks without any mortality in 30% sea water, those in PARRY's experiments lived for 45 hours only. Furthermore newly hatched salmon alevins lived for a week in 50% sea water while they lived for only 45 hours in PARRY's experiments.

The behaviour of salmonid alevins to different salinities suggests that they are able to survive a salinity of 25% sea water for longer periods as compared to what is previously recorded. At this salinity they live without any mortality for 10 weeks (the duration of the experiment). At 30% sea water they live from 4–10 weeks. It is concluded that salmonid alevins can live for long periods in salinities up to 9·84 $^0/_{00}$ (30% sea water) without any apparent ill-effects. This salinity tolerance may be explained as due to the ability of the alevins for osmoregulation in different salinities. This osmoregulation may be due to:—

(1) The impermeability of the outer surface of the body which seems to be more efficient than that found by PARRY (1958 and 1960). PARRY found that salmonid alevins had some degree of impermeability which breaks after a time interval almost irrespective of salinity. This was not the case in the present investigation as shown by the results in Figure 4 where the median survival time of salmon was 70, 18, and 7 days at 30, 40, and 50% sea water respectively. It is concluded that the degree of impermeability is dependent on the external salinity, being less in higher salinities. Thus the outer skin may play a more important rôle in osmoregulation at different salinities than what was previously believed. BLACK (1957) concluded that the control of permeability may be the result of neurosecretory or hormonal reaction to the new environment, and it may also be the result of a direct effect on the surface cells. In addition, the presence of calcium ions in the outer medium decreases cell permeability.

(2) The development of acidophile cells (Keys-Willmer) in the gills may be an important factor in increasing the efficiency of osmoregulation (LIU, 1942; VICKER, 1958). PARRY (1960) pointed out that acidophile cells are present in salmonid alevins from a very early stage (4 weeks old). However, PARRY, HOLLIDAY, and BLAXTER (1959) did not find any clear evidence that these cells are salt regulating.

Although measuring of the freezing-point depression gives a precise information of the internal changes which take place within the fish after being exposed to different salinities, PARRY's (1960) measurements were restricted to salmonid

alevins subjected to 100% sea water. This study was not extended to alevins living at lower salinities. Furthermore, the temperature may have an effect on the salinity tolerance of fish. Thus the differences between Parry's (1960) results and those obtained in the present investigation, may be attributed — among other factors — to the differences in the experimental temperatures. While Parry carried out her experiments at 10°–12°C my experiments were done at 4·5°–6·5°C. Investigations on the effect of temperature on salinity tolerance in fish needs further work.

The feeding condition and nature of food may play an important rôle in the salinity tolerance of salmonids. The death of 6 week-old post-hatch salmon alevins in Parry's experiments (1960) in different dilutions of sea water, may be attributed to the starvation of these fish. Parry (1960) mentioned that she used starved fish and did not give the duration of her control experiments. In the present investigation salmonid alevins lived in 25% sea water for at least 5 weeks after the yolk-sac absorption, where they were well fed with the digestive gland of the shore crab *Carcinus maenas* and *Daphnia* sp.

From the present results it is concluded that salmonid alevins have an efficient mechanism by which osmoregulation is maintained for long periods in low salinities (i.e. 30% sea water).

Salmonid alevins die if subjected to sea water of $33^0/_{00}$ salinity for more than 10 hours, salmon being more resistant than brown trout and sea trout. A similar observation was recorded by Bert (1871); Hays (1926); McGonigle (1929); Chaisson (1934); Busnel, Drilhon, and Raffy (1946); and Parry (1960). The death of fish at high salinities may be due to the upset of the respiratory mechanisms (Bert, 1871; Fage, 1912). However, Raffy (1932) concluded that asphyxia is not the main cause of death. Leövey (1938) attributed the death of marine teleosts at higher salinities, to inability of the gills to secrete excess salts as well as to the salt accumulation in the tissues.

My results confirm the earlier findings of Busnel, Drilhon, and Raffy (1946) who found that the absorption of the yolk-sac at 30% sea water took place at a slower rate than at lower salinities. During rearing of salmonids it was found that water of low salinity (up to $8^0/_{00}$) is favourable, and the fish are healthier and lived better than those reared in fresh water. This is attributed to the death of parasites attacking the alevins in such low-salinity water. Ramult (1927) found that salmon alevins may live in the Baltic at a salinity of $16–17^0/_{00}$. Busnel (1943) concluded that rainbow trout survives better in brackish water.

Acknowledgements

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Summary

1. Newly hatched herring larvae can live at salinities as low as 2·5 $^0/_{00}$. They live better and longer in salinities from 10–15 $^0/_{00}$ than in higher or lower salinities.

2. Lump-sucker larvae can live for at least 14 days at 9 $^0/_{00}$ salinity. Salinities below 5 $^0/_{00}$ prove fatal within less than 24 hours. Acclimation to low salinities, although causing an increase in the resistance time, does not seem to affect the lower lethal limit of salinity (i.e. 5 $^0/_{00}$).

3. Young plaice (38–50 mm long) can live at low salinities of 5 $^0/_{00}$ for at least ten days. Lower salinities can be tolerated for a few days. Even fresh water has no ill-effects on the fish for about 20 hours.

4. Salmon, sea trout, and brown trout alevins can live for at least 10 weeks at salinities up to 9·20 $^0/_{00}$ (25% sea water). At a salinity of 9·84 $^0/_{00}$ (30% sea water) salmon is more tolerant than brown trout and sea trout. Brown trout is more resistant as compared with sea trout. At 40% sea water salmon alevins show more resistance and can live for 18 days while sea trout and brown trout can live for 9 and 11 days respectively. At 50% sea water the alevins of the three species live for about one week.

5. The resistance of salmon, sea trout, and brown trout to salinity changes seems not to change while the yolk-sac is not completely absorbed.

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The Effectiveness of Sampling Methods Used to Study the Distribution of Larval Herring in the Gulf of Maine

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Introduction

In 1956, 1957, and 1958, the Fisheries Research Board of Canada and the United States Fish and Wildlife Service conducted cooperative cruises to study the early life history of herring in the offshore areas of the Bay of Fundy and the Gulf of Maine, (TIBBO, *et al.*, 1958). The purpose of that investigation was to determine spawning and nursery areas, to obtain information on survival, growth, and dispersal of larvae, and to study the relationship of spawning and larval drift to the abundance of "sardine" herring in the inshore areas of Maine and New Brunswick.

The work of TIBBO, *et al.* (1958), was based on macroscopic examination of metre-net and Hardy Plankton Recorder material. In the present paper a more detailed analysis of the data is made to determine the efficacy of the sampling techniques in programmes of this nature.

Materials and Methods

For this analysis only material from United States Fish and Wildlife Service cruises of September, October, November 1956, and January, February 1957, has been included as the coverage during these cruises was more complete than that of any other series. The sampling gear used was the Hardy Plankton Recorder (HARDY, 1936) and 1 m ring-nets. Hardy Plankton Recorders were towed continuously at the surface and at 10 m at a speed of approximately 10 knots. The recorders were equipped with a 3/4 inch square mouth opening and 60 mesh-per-inch filtering silk. The propellor setting was such that each 2 inch section of filtering silk represented approximately 5 miles of tow (3·4 cubic metres of water filtered). Fifteen-minute oblique metre-net tows (10 m to

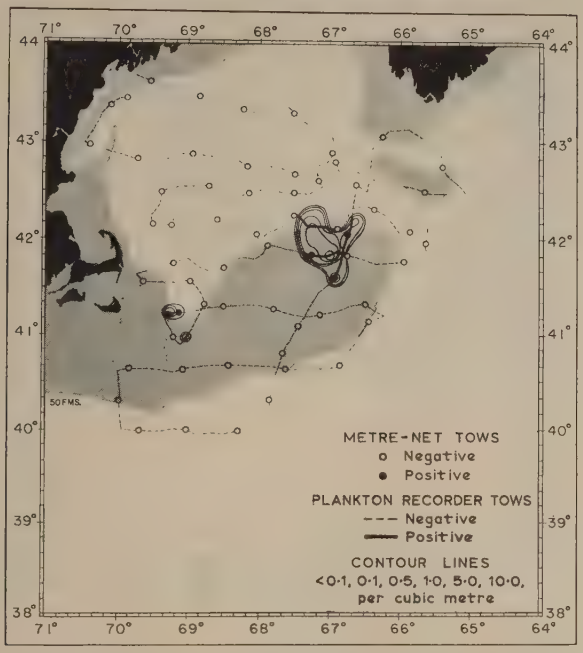

Figure 1. The abundance and distribution of larval herring, "Silver Bay" Cruise No. 1, 21. September–5. October 1956.

surface) were made every 4 hours. The nets were constructed of No. 0 silk or nylon and the towing speed was about 3 knots. Larval fish of all species were removed, counted, and measured. All lengths recorded in this paper are total lengths and all numbers are in terms of numbers per cubic metre of water filtered.

Distribution, Abundance, and Length of Larval Herring

Charts showing cruise lines and the distribution and abundance of larval herring as determined by metre-net and Hardy Plankton Recorder samples for September, October, and November 1956, and January and February 1957, are presented in Figures 1, 2, 3, 4, and 5. The abundance figures for the Hardy Plankton Recorder material are an average of the catch at the surface and at 10 m.

The distribution of larval herring as determined by Hardy Plankton Recorder material is in general of a more detailed nature than that indicated by metre-net tows. This is due largely to the continuity of the Hardy Plankton Recorder sample. In several instances larvae were caught by the recorders and not by the metre net, but usually the differences in distribution as indicated by the two sampling methods are due to the fact that the Hardy Plankton Recorder caught larval herring in areas not sampled by the metre nets. There are, however,

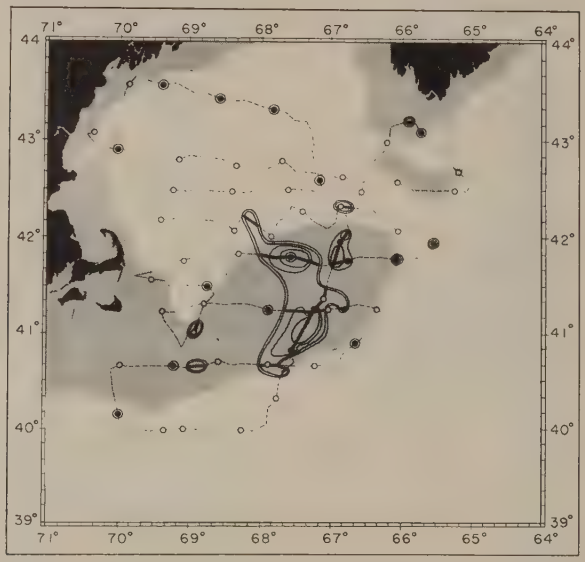

Figure 2. The abundance and distribution of larval herring, "Silver Bay" Cruise No. 2, 15.–25. October 1956.

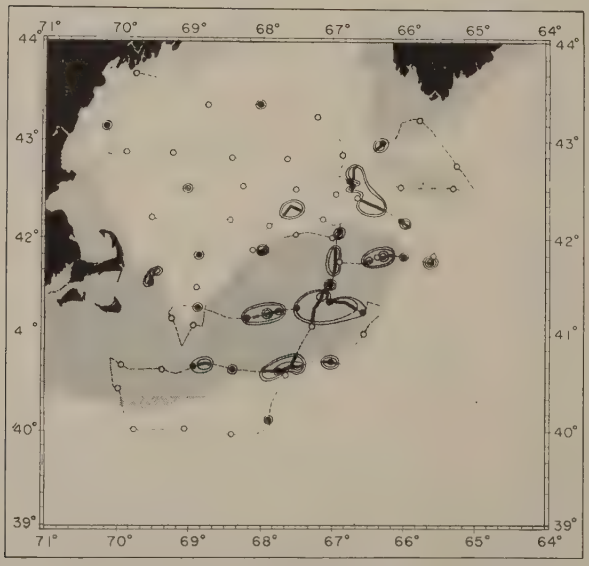

Figure 3. The abundance and distribution of larval herring, "Silver Bay" Cruise No. 4, 14.–30. November 1956.

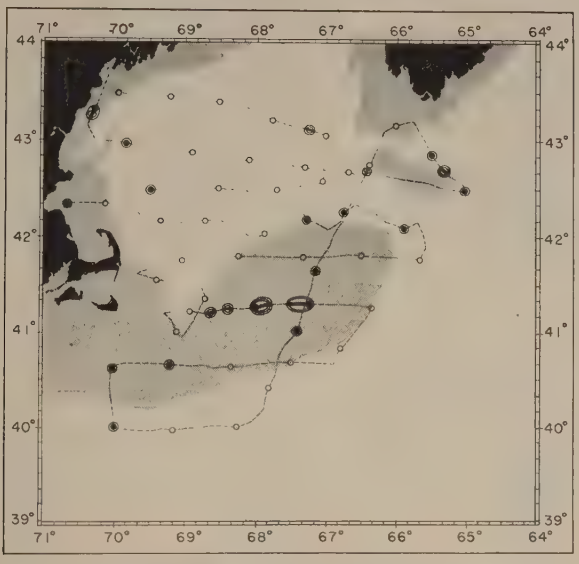

Figure 4. The abundance and distribution of larval herring, "Delaware" Cruise No. 57–1, 28. January–4. February 1957.

Figure 5. The abundance and distribution of larval herring, "Albatross" Cruise No. 88, 19.–28. February 1957.

Table 1

Comparison of the average number of larval herring per m^3 as indicated by Hardy Plankton Recorder and metre-net samples

	Plankton Recorder	Metre net
"Silver Bay" Cruise No. 1	·100	·080
"Silver Bay" Cruise No. 2	·060	·090
"Silver Bay" Cruise No. 3	·040	·020
"Delaware" Cruise No. 57–1	·008	·003
"Albatross" Cruise No. 88	·011	·002
Average	·044	·039

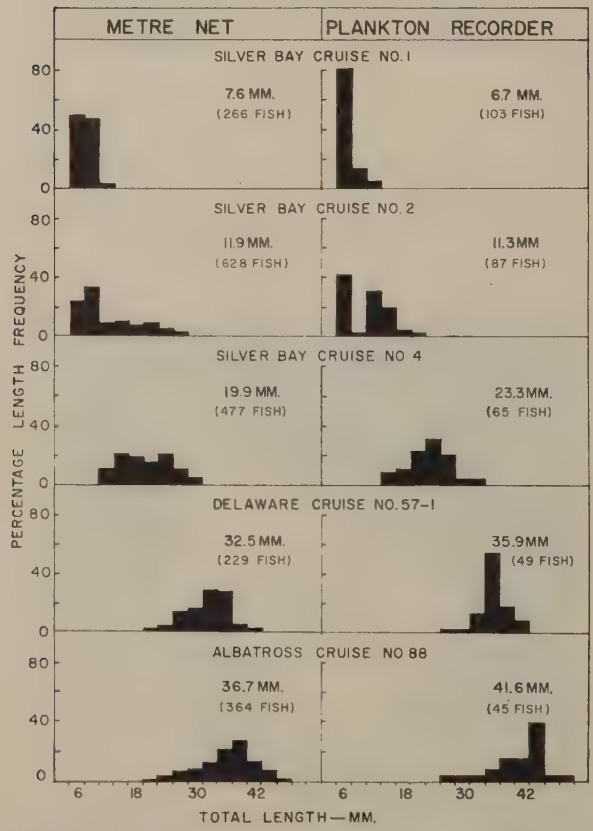

Figure 6. Length frequency and average length of herring larvae, September, October, November 1956, and January, February, 1957. Data are combined in 3 mm size groups.

many cases where concentrations of larval herring are indicated in the metre-net samples and not in the Hardy Plankton Recorder material. In all but two of these tows ("Silver Bay" Cruise No. 2) the concentration of larval herring was less than 0·1 per m^3. The small volume of water filtered by the Hardy Plankton Recorder in a 5-mile tow is not sufficient to indicate the presence of larvae in such slight concentrations.

In all cruises except "Silver Bay" No. 2 the average abundance of larval herring as indicated by the Hardy Plankton Recorder material was greater than that indicated by the metre-net collections (Table 1). The ratio of the number of larvae per cubic metre caught in the Hardy Plankton Recorder to that caught in the metre net increased with time and with length of larvae.

In Figure 6 the length frequency and average length of herring larvae caught in the Hardy Plankton Recorder and metre net are shown. With the exception of "Silver Bay" Cruises Nos. 1 and 2, the average length of recorder-caught larvae was significantly greater than the average length of larvae caught in metre-net tows. These differences in average length are most likely due to greater escapement of the larger larvae from the relatively slow-moving metre nets. Such a variation in the average length of larvae results in a marked difference in the approximate measure of growth obtained by plotting average lengths of larvae caught by the recorder and metre net during each month.

Diurnal Variation in Abundance and Length

Tibbo, *et al.* (1958), noted that greater numbers of larval herring were taken in 1 m nets during the night than during the day, that the proportion of larvae caught during the night increased with an increase in length of the larvae, and that the ability of the larger larvae to avoid capture accounted for such variations. Bridger (1956) demonstrated an increase in the night/day ratio of larval herring taken in vertical Helgoland net hauls with an increase in larval size and the ability of the larvae to escape slow-moving nets. The high speed of tow reduces the effect of escapement in Hardy Plankton Recorder sampling.

Surveys of the Georges Bank area during 1953, 1955, and 1956 showed that although the night catches of larval haddock, cod, hake, and flounder species in metre-net tows were markedly greater than the day catches, there was no appreciable variation in the average number or length of larvae caught in the Hardy Plankton Recorders during the day and night (Colton, unpublished data). During the survey under discussion, however, the night/day ratio of larval herring taken in the metre net and the Hardy Plankton Recorder is similar (Table 2).

With the exception of the prolarvae[1]) caught in the metre-net tows of "Silver Bay" Cruises 1 and 2 and the Hardy Plankton Recorder tows of "Silver Bay" Cruise 1, the greater percentage of herring larvae was taken during the night. The average length of the larvae in both the metre net and recorder was also generally greater during the night than during the day. This increase in abun-

[1]) The following allocation proposed by Hubbs (1943) was used in the separation of the early stages of fish:—

Prolarva = Larva still bearing yolk.
Postlarva = From absorption of yolk to time when adult characteristics assumed.

Table 2

Percentage abundance and average length of larval herring during the day (sunrise to sunset) and night (sunset to sunrise)

	Metre Net				Plankton Recorder			
	Day		Night		Day		Night	
	%	Average length (mm)	%	Average length (mm)	%	Average length (mm)	%	Average length (mm)
"Silver Bay" Cruise No. 1	79	6·1	21	9·0	94	6·1	6	6·9
"Silver Bay" Cruise No. 2	93	6·8	7	13·3	35	7·2	65	14·1
"Silver Bay" Cruise No. 4	2	19·4	98	18·4	28	20·9	72	22·6
"Delaware" Cruise No. 57–1	1		99	32·2	6	32·0	94	36·1
"Albatross" Cruise No. 88	1	30·0	99	39·6	0		100	42·1
Average	35		65		33		67	

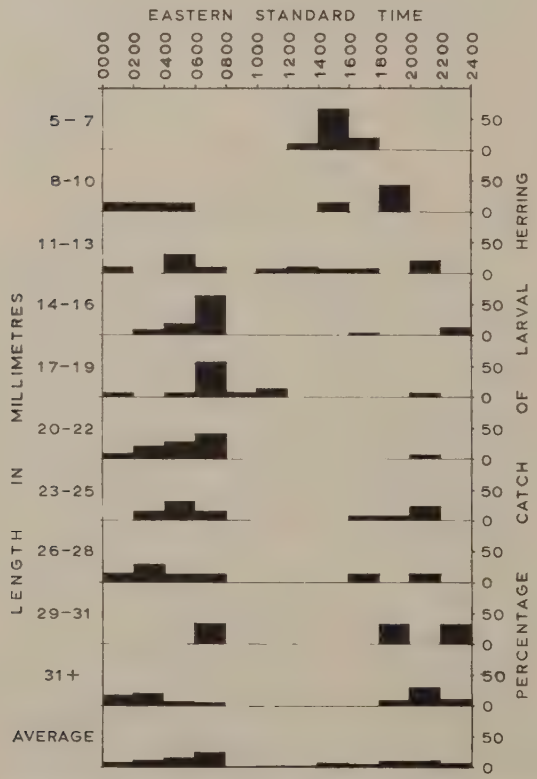

Figure 7. Percentage Recorder catch of larval herring by time, September, October, November 1956, and January, February 1957. Time is Eastern Standard Time.

dance and size during the night in the metre-net material is undoubtedly due in part to escapement of the larger larvae during the day, but the fact that there is also an increase in the average size and abundance during the night in the recorder catches indicates that larval herring move up to the surface layers during the night and that the magnitude of these diurnal movements increases with the size of the larvae.

That diurnal migration of herring does occur is evidenced by a comparison with the day and night catch of red hake (*Urophycis chuss*) during these cruises. In abundance and size range (3·5–45·0 mm) this species was similar to the herring. In the metre-net catches, the day and night distribution was similar to that of the herring (day, 32%; night, 68%), but in the recorder equal numbers were caught during the day and night (day, 49%; night, 51%). The average size of the red hake caught in the metre net was greater during the night than during the day, but of equal size during the day and night in the recorder. Thus escapement does not appear to be the only cause for the variation in the abundance of larval herring during the day and night.

In Figure 7 the percentage of the total recorder catch of larval herring in 3 mm length groups for 2-hour time intervals is shown. The average time of sunrise was 0634 and the average time of sunset was 1717 (Eastern Standard Time). With the exception of the 5–7 mm larvae caught during September more larval herring of all size groups were caught during the night. No larval herring larger than 19 mm were caught during the daylight hours. The maximum catches tended to occur just before sunrise. The predominance of the 5–7 mm larvae in the daylight hours appears to be due to inadequate sampling, as these recently hatched larvae were concentrated in a small area on the northern edge of Georges Bank (Fig. 1), which was only sampled during the daytime. The fact that they were captured during the day in both the metre net and the recorder, however, indicates that prolarvae and early postlarvae are physically incapable of undertaking appreciable horizontal or vertical movements and that adequate sampling would show equal abundance during the day and night.

The data on day and night distribution coupled with the fact that more larvae were caught in the recorder towed at the 10 m level in both day (87%) and night (76%) indicate that postlarval herring only occur in appreciable numbers in the surface layers during the night, that the extent of this diurnal migration increases with the size of the larvae, and that the depth of maximum abundance is below the 10 m level.

Discussion

This analysis reveals two aspects of the behaviour of larval herring, namely escapement and diurnal migration, that must be considered before any attempt is made to estimate quantitatively their abundance and distribution. The ability of the larger larvae to avoid slow-moving nets during the daylight hours has been previously demonstrated by Bowers (1952) and Bridger (1956) and is further evidenced by the greater average size of larvae caught in the recorder than those caught in the metre net. Diurnal vertical movements of juvenile, immature, and mature herring have frequently been observed on both sides of the Atlantic (Moore, 1898; Lucas, 1936; Johnson, 1939; and Richardson, 1952). Diurnal changes in the depth of larval herring, however, have not been

Figure 8. Day and night distribution of larval herring, November 1956, and February 1957.

conclusively demonstrated although BRIDGER (1958) on the basis of horizontal tows at 4, 10, and 17 fms with a modified Gulf III high-speed tow net showed that in full daylight the bottom yielded a higher proportion of older postlarvae (16–25 mm).

The effect of escapement and diurnal migrations upon the distribution pattern as determined by metre-net and recorder sampling in the upper 10 m of water is clearly shown in Figure 8. Here the plot of the distribution of herring larvae during November 1956, and February 1957, is superimposed on a track chart showing the periods of daylight (sunrise to sunset) and darkness (sunset to sunrise). With only a few exceptions, all catches of larval herring were made at night or within a few hours after sunrise. What is plotted is not a picture of the distribution over the whole area, but of the distribution at night. Herring most likely occurred in many areas other than those indicated.

The data suggest that in order to sample larvel herring effectively it is necessary to employ high-speed nets. Of the two sampling methods used, the Hardy Plankton Recorder, because of its high speed and continuity of tow, gives the better estimate of abundance and distribution. The magnitude of the recorder sample is not sufficient, however, for detailed analysis of growth and mortality. Secondly, the data indicate that the vertical distribution of larval herring changes during the day and night and that the depth of maximum abundance is below the depth sampled during these cruises (10 m).

Bridger (1958) overcame these two limitations through the use of oblique Gulf III tow-net hauls and concluded that diurnal migration of postlarval herring is unlikely to affect their capture provided that the oblique haul is made to within 2 fms of the sea bed. Although it appears that in relatively shoal water oblique high-speed tows would be a more suitable sampling method, it will be first necessary to determine accurately the depth distribution of larval and postlarval herring over the whole water column and the extent of their diurnal vertical migrations. For such a study it is essential to use high-speed samplers that can be towed in series down to considerable depths (100 m) and that filter enough water to give samples of sufficient size for statistical analysis. Such a programme of study is now being undertaken at this laboratory.

Summary

1. An analysis was made of metre-net and Hardy Plankton Recorder tows used in the study of the distribution and abundance of larval herring in the Gulf of Maine.

2. A greater average abundance of larval herring and a more detailed picture of distribution was indicated by the Hardy Plankton Recorder data than by the metre-net collections.

3. The ratio of the number of larvae per cubic metre caught in the Hardy Plankton Recorder to that caught in the metre-net increased with an increase in the length of the larvae.

4. The average length of larvae taken in the Recorder was greater than the average length of larvae caught in metre-net tows, and this variation was shown to be due to escapement of the larger larvae from the metre net during the daylight hours.

5. The number and average length of larval herring and red hake were greater at night in the metre-net catches, while the number and length of herring larvae but not red hake were greater at night recorder catches. Thus, differences in the day and night catch of larval herring are not due solely to daytime escapement of the larger larvae, but also to the fact that larval herring move up to the surface layers during the night.

6. In the recorder more larval herring were caught at 10 m than at the surface during both the day and night and there was an increase in the night/day ratio with an increase in larval size. These observations indicate that the depth of maximum abundance of larval herring is below 10 m and that the extent of diurnal migration increases with an increase in the size of the larvae.

7. It is demonstrated that a true picture of the distribution of larval herring is not obtained by either the metre-net or the Hardy Plankton Recorder samples when such sampling is confined to the upper 10 m of water.

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The Selection Characteristics of Nylon Gill Nets for *Tilapia esculenta* Graham

By

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Introduction

Few types of fishing gear will capture fish throughout the length range of a species and it is therefore essential to define the size selection characteristics of the gear before catch data can be used for population studies.

This is particularly true of fishing gears that depend upon the action of a net mesh. In trawl and seine net fisheries there is a lower limit to the length range of fish caught below which individuals are able to escape through the mesh: gill nets are doubly selective in that there is also an upper size limit to the probability of capture where a fish is so large as to be unable to penetrate the net mesh far enough to be captured. Between these limits the length-frequency distribution of gill-net catches of a single species may be approximately normally distributed with a mode at a length where the girth of the fish is approximately equal to the circumference of the net mesh.

Holt (1957) described a general method for defining the selection characteristics of gill nets. This has been applied to a number of species in temperate waters and, in particular, studies of herring (Richardson, 1956) and salmon (Olsen, 1959) have shown that the theory may require some modification according to the species being considered. Richardson showed that the selection curve of drift nets for North Sea herring may have more than one mode because the fish may become enmeshed in one of three positions. Olsen showed that the gill-net selection curves for North Atlantic herring are slightly skewed. This worker also describes a method for the adjustment of gill-net catches in order to obtain a true length-frequency distribution of the population.

The commercial fisheries of Lake Victoria, East Africa, are based primarily upon the use of gill nets. African fishermen are not equipped with vessels that can fish other types of gear, so that a knowledge of the size distributions of the fish population of Lake Victoria is almost entirely dependent upon the interpretation of commercial and experimental gill-net fishing records. In this paper the method described by Holt is applied to data for a tropical species, *Tilapia esculenta* Graham. The selection characteristics of nylon nets for this species also show certain features that necessitate a modification of the general theory.

The General Theory of Gill-Net Selectivity

Assuming that the growth of a fish is isometric, then the selection for length by a given mesh size may be expected to be normally distributed.

When two gill-net units, A and B, are fished simultaneously then the logarithm of the ratios of the catches at successive length groups in the two units will have a linear relationship provided

(i) that the units differ only very slightly in mesh size (i.e. have widely overlapping selective ranges),

(ii) that the standard deviation of the selection curve is the same for both units.

The two selection curves will intersect at the length where the ratio is unity and if a series of gill-net units are operated simultaneously the graph of this length against the average mesh size will be linear, passing through the origin. The mean retention lengths of each mesh size are related in the same way and can be calculated from the relationship.

The standard deviation of the selection curves can then be calculated from the expression

$$\sigma = \sqrt{\frac{B^L M^2 - A^L M^2}{2a}} \; *)$$

where $A^L M$, $B^L M$ are the mean retention lengths of the gill-net units A and B.

a is the y intercept of the graph of the logarithms of the ratios of catches at successive length groups.

Materials

The material for an analysis of the selectivity of gill nets for *T. esculenta* is restricted to the size range 20–35 cm. Fish of smaller sizes occupy a totally different habitat and are difficult to locate in quantity until they move to inshore areas under the stimulus of maturation at 20–25 cm total length (LOWE [MCCONNELL], 1956). Mature fish of all sizes occupy the same general habitat and constitute the fishable stock, but owing to market preferences, only *T. esculenta* exceeding 26 cm in length are exploited commercially. This has now led to a marked division in abundance of the unexploited and exploited phases of the fishable stock. This is demonstrated in Table 1, the material upon which this analysis is based: the average catch per net of nets fishing the commercially unexploited phase was 6·9 fish; whereas 11·2 cm (4·8 inch) nets, used commercially, returned 1·7 fish per net during this experiment.

The material was obtained from routine fishing of a gill-net fleet containing 3 × 8·1 cm, 3 × 9·1 cm, 3 × 9·6 cm, 6 × 11·2 cm, and 4 × 12·3 cm mesh nets. The number of settings in Table 1 refers to individual nets, the discrepancies in numbers being caused by the occasional addition or removal of single nets for maintenance purposes. Owing to the scarcity of fish caught in 11·2 cm and 12·3 cm nets it was necessary to include data from fishings of 10·2 cm, 11·2 cm, and

*) This formula differs from that given in HOLT's paper by the inclusion of 2 in the denominator which was omitted in the original publication.

Table 1

The material used for the estimation of the selection curves of nylon gill nets for *Tilapia esculenta*

Length group (cm)	Number of fish/Mesh size (cm)					
	8·1	9·1	9·6	10·2	11·2	12·3
18·5	7	–	–	–	–	–
19·5	90	1	–	–	–	–
20·5	199	9	–	–	–	–
21·5	182	53	3	–	–	–
22·5	119	290	11	1	–	–
23·5	29	357	66	7	–	–
24·5	17	225	178	26	–	–
25·5	3	82	202	69	–	–
26·5	–	19	77	125	15	–
27·5	–	10	29	134	73	2
28·5	–	–	4	81	117	7
29·5	–	–	2	20	107	20
30·5	–	–	–	11	40	25
31·5	–	–	–	–	15	33
32·5	–	–	–	–	2	15
33·5	–	–	–	–	–	6
Total fish	646	1046	572	474	369	108
Net settings	101	125	104	196	221	153

N.B. All mesh sizes are taken as stretched mesh measured over 26 meshes under 2·27 kg (5 lbs) stretch tension.

12·3 cm mesh sizes during 1957/1958 and consequently the analysis has been divided into the selectivity of 8·1 cm, 9·1 cm, and 9·6 cm meshes, and 10·2 cm, 11·2 cm, and 12·3 cm meshes. Gill nets of 10·2 cm mesh were included in the 1959 fleet but were found to be 9·6 cm in actual fact. Hence there are no data for 9·6 cm and 10·2 cm meshes fished simultaneously and the range of overlap of the selection curves of 9·6 cm and 11·2 cm mesh sizes is not adequate to permit comparison.

The nets used were 91·4 m long and hung by the half (i.e. 50 yds long in the water). All nets were 26 meshes deep thus giving a different effective area to each mesh size. Personal observation has shown that almost all fish are caught within one metre of the bottom and Iles (personal communication) has shown that the difference in area has no significant effect upon the catch per net yield of *Tilapia* species in Lake Nyasa. Differences in the depth of nets of successive mesh sizes have been disregarded, since trial corrections to the present data gave no improvement in the interpretation.

The nets, which fished on the bottom, were laid twice weekly in the late afternoon and lifted the following morning.

The fish caught were measured to the nearest half-centimetre below for the total length between the tip of the lower jaw and the tip of the dorsal ray of the caudal fin horizontally extended. These data were later aggregated to the nearest centimetre below because there was some indication of bias in the measurement of the x·5–x·9 cm groups. Girth measurements were taken vertically between the pelvic girdle and the first dorsal fin ray, i.e. just posterior to the operculum in this species.

Throughout the period when the data were collected there was some loss

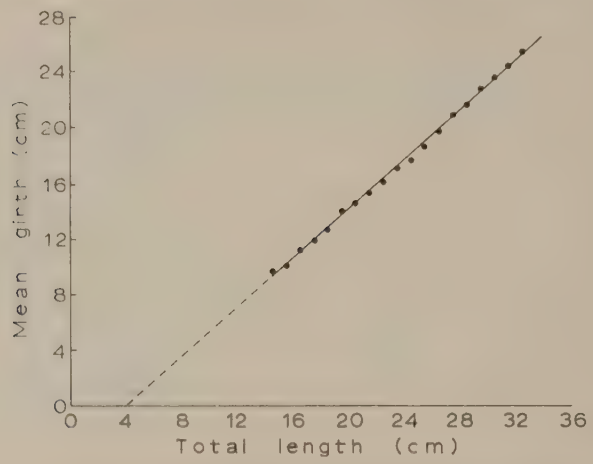

Figure 1. The girth/length relationship for *Tilapia esculenta*.

Table 2

A comparison of mesh circumference and mean girth size

Mesh (cm)	Circumference	Mean girth of fish captured	Girth/Mesh circumference
8·1	15·2	14·7	·97
9·1	17·8	16·9	·95
9·6	19·0	18·2	·96
11·2	22·9	23·6	1·03

through predation by *Protopterus* when fish were in the nets. These "predators" take fish indiscriminately, regardless of size, and hence no correction has been possible.

The Application of General Theory to Data for *T. esculenta*

A fish is captured in a gill net by passing through the mesh to a point where its girth is approximately equal to the net mesh circumference so that the fish is held unless it is able to withdraw. The susceptibility of a fish to capture by a given mesh size is therefore dependent upon its girth (Table 2) and the length range taken is related to the girth/length relationship of the species.

Figure 1 shows this relationship for *T. esculenta*. The girth was measured between the pelvic fins and the first dorsal fin ray, the point at which this species is most commonly retained by a gill net. This relationship has the regression

$$\text{Girth} = 0{\cdot}88\ (\text{length}) - 3{\cdot}5$$

but there is some departure from linearity in the length range 22–26 cm.

The standard deviation of the data are given in Tables 3 A and 3 B.

Table 3

A. The standard deviation of girth

Length (cm)	Standard dev. of girth (cm)	Number of observations	Length (cm)	Standard dev. of girth (cm)	Number of observations
20·5	0·48	81	26·5	0·73	93
21·5	0·66	83	27·5	0·70	89
22·5	0·71	117	28·5	0·65	95
23·5	0·55	117	29·5	0·81	83
24·5	0·63	115	30·5	0·77	87
25·5	0·79	115	31·5	0·85	80

B. The standard deviation of length

Girth (cm)	Standard dev. of length (cm)	Number of observations	Girth (cm)	Standard dev. of length (cm)	Number of observations
16·0–16·9	0·81	150	20·0–20·9	0·70	81
17·0–17·9	0·83	164	21·0–21·9	0·82	110
18·0–18·9	0·70	114	22·0–22·9	0·88	84
19·0–19·9	0·60	88	23·0–23·9	0·86	101

C. Standard deviations of bivariate distributions of girth and length within the catch of one gill-net mesh size

Net mesh (cm)	Standard dev. of length (cm)	Standard dev. of girth (cm)	Number of observations
8·1	1·24	1·10	140
9·1	1·19	1·02	296
9·6	1·03	·88	154
11·2	1·86	1·71	85

Figure 2 shows the logarithmic plots of the catch ratios of each mesh comparison. Although all are S-shaped to some degree they can be approximated by linear regressions over the greater part of their range. The equations of these regressions are given in Table 4.

From HOLT's theory, the plot of a/b against the average mesh size, i.e. the length at intersection of adjacent distributions, is linear if there is no trend in the standard deviation with increasing mesh size. The mean retention lengths are related by the same function and can be calculated from the regression equation.

The data for *T. esculenta* plotted in this way are shown in Figure 3 which has the equation

$$L_M = 5{\cdot}59 \text{ (mesh size)} + 4{\cdot}01$$

It will be noted that the intercept, 4·01, corresponds very closely to the intercept of 3·98 of the girth/length relationship where the girth is zero.

The mean retention lengths and standard deviations of the selection curves for 8·1 cm, 9·1 cm, 11·2 cm, and 12·3 cm meshes calculated by the method are given in Table 5.

The linearity of the 9·1cm/8·1cm mesh comparison indicates that over the range considered the selection curves of these meshes are normally distributed and have the same standard deviation. The sigmoid form of the 9·6 cm/9·1 cm

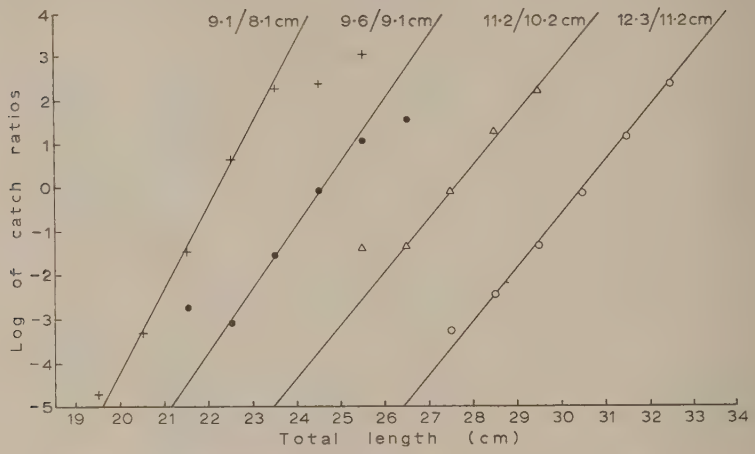

Figure 2. The logarithmic plots of the ratios of catch per net in gill nets with overlapping selection ranges.

Table 4

Linear regression equations of the logarithmic plots of catch ratios (fitted by least squares)

Mesh comparisons	Equation	a/b	Range considered (cm)
9·1/8·1	$y = 1{\cdot}90x - 42{\cdot}25$	22·20	20·5—23·5
9·6/9·1	$y = 1{\cdot}48x - 36{\cdot}30$	24·58	22·5—25·5
11·2/10·2	$y = 1{\cdot}22x - 33{\cdot}60$	27·60	26·5—29·5
12·3/11·2	$y = 1{\cdot}21x - 36{\cdot}96$	30·50	28·5—32·5

mesh comparison must therefore be caused by asymmetry of the 9·6 cm mesh selection curve. However, a linear regression can be taken at the point of intersection of the 9·6 cm and 9·1 cm mesh selection curves indicating that over a limited range the curve for the 9·6 cm mesh is sufficiently normally distributed to permit its use in the calculation of parameters for 8·1 cm and 9·1 cm meshes. The parameters for 9·6 cm mesh itself have been omitted. Those of the 10·2 cm mesh have also been omitted for similar reasons.

This sigmoid asymmetry of the regressions occurs at the limits of the selection curves where the numbers of fish caught is greater than would be expected if the length-frequency distributions of the gill-net catches were normal throughout their range. The selection curves of data from flax gill-net catches have been shown to be normally distributed (BEVERTON, 1957). This suggests that the asymmetry observed in the distributions of catches in nylon nets is caused by the increased tendency of fish to become entangled by synthetic fibres. The present data are not adequate to permit an accurate analysis of this portion of the selection curves.

The method described by HOLT (1957) requires that at least four gill nets of overlapping selection ranges must be operated in order to obtain a minimum of three comparisons. In some species, where certain size groups have specific

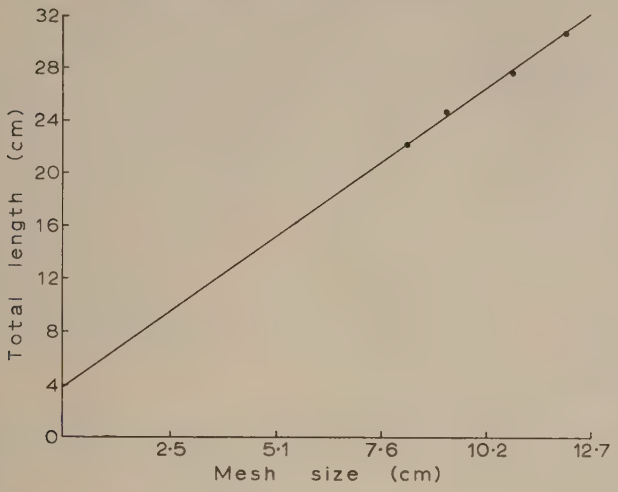

Figure 3. The plot of a/b against mesh size.

Table 5

The parameters of the gill-net selection curves calculated from general theory and algebraically

Mesh size (cm)	Holt's Method M. R. L. (cm)	(cm)	Algebraic Method M. R. L. (cm)	(cm)
8·1	20·8	1·20	21·0	1·16
9·1	23·6	1·20	23·5	1·16
11·2	29·2	1·48	29·3	1·57
12·3	31·9	1·48	31·7	1·57

habitat preferences, this may not be possible because the size range available in one habitat is inadequate. Similarly a restricted size range occurs in some cichlid species where growth is extremely slow following the onset of breeding.

For *T. esculenta* an analogous situation obtains owing to the division in abundance of the unexploited and exploited phases of the fishable stock. The commercial fishermen of Lake Victoria fish 11·2 cm gill nets which catch fish at lengths exceeding 25 cm. It has been shown that there is a very marked change in the relative abundance of fish of size groups below and above this limit, which lies within the selection range of the experimental gill nets of 9·1 cm and 9·6 cm.

With data of this form it is valuable, and in some cases necessary, to determine the selection characteristics of the gear from two pairs of comparisons only, i.e. three gill-net mesh sizes. The mean retention length and standard deviation of such distributions can be calculated algebraically from HOLT's theory provided that the regression of both comparisons are linear. This indicates, by definition, that there is no trend in the standard deviation of the three meshes over a greater proportion of their range.

From HOLT's general theory:— $\sigma = \sqrt{\frac{B^L M^2 - A^L M^2}{2a}}$

which, when expanded, becomes

$$\sigma = \sqrt{\frac{(B^L M - A^L M)(B^L M + A^L M)}{2a}} \tag{1}$$

therefore since

$$2^a/_b = A^L M + B^L M$$

$$A^L M = \frac{(2^a/_b)^2 - 2a\sigma^2}{4^a/_b}$$

In a comparison of gill nets A and B

$$B^L M = 2^a/_b - A^L M$$

which is equal to the mean retention length of the smaller mesh of a comparison of gill nets B and C.

Thus

$$2^{a_1}/_{b_1} - \left[\frac{(2^{a_1}/_{b_1})^2 - 2_{a_1}\sigma^2}{4^{a_1}/_{b_1}}\right] = \frac{(2^{a_2}/_{b_2})^2 - 2a_2\sigma^2}{4^{a_2}/_{b_2}} \tag{2}$$

by the substitution $p = {}^{a_1}/_{b_1}$ and $q = {}^{a_2}/_{b_2}$

this expression becomes

$$\sigma = \sqrt{\frac{{}^q/_p(2p)^2 + (2q)^2 - 8pq}{2(a_2 + {}^q/_p a_1)}} \tag{3}$$

The mean retention lengths can then be calculated from expression (1) by substitution of the value obtained for the standard deviation of the catch distributions.

The parameter values calculated algebraically are compared to those obtained by HOLT's method in Table 5.

The fit of the observed distribution to the theoretical distribution (based upon parameters calculated by the algebraic method) are illustrated in Figure 4, for 8·1 cm and 9·1 cm meshes. The higher abundance of the 22·5 cm group is shown by both meshes.

The validity of these two sets of estimates can be tested and compared using the method described by OLSEN (1959).

When the selection curves of two gill nets overlap, the catches in each length group should give very similar length-frequency distributions for the population when corrected for the selection factors for the particular mesh used.

In short-term fishing experiments the numbers encountered by each mesh size may not be comparable (as is necessary in the initial analysis) but the proportional change in abundance of each length group will be the same for each mesh.

The true density of any length group as given by Cl/Sl where Cl is the number caught and Sl is the selection factor for that gill net at length, l, expressed as a percentage of the maximum efficiency at the mean retention length of the mesh.

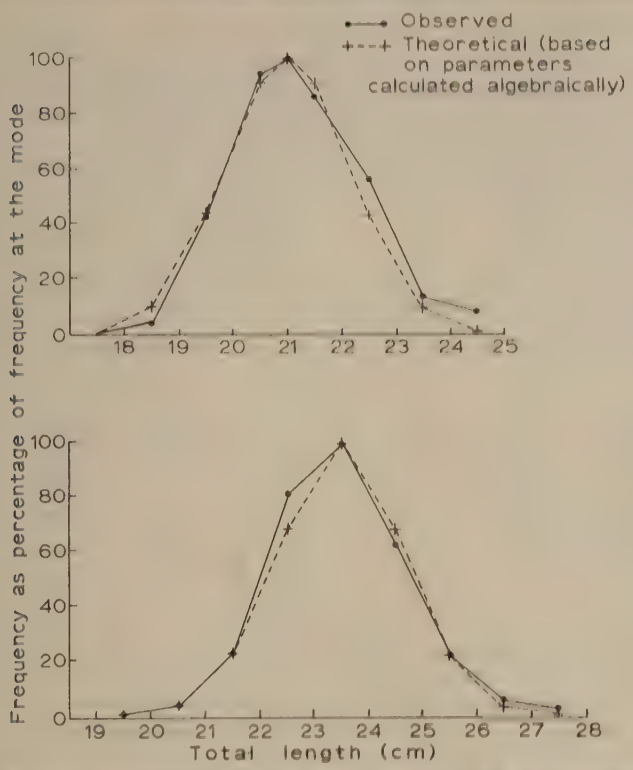

Figure 4. A comparison of the observed and theoretical length-frequency distributions of 8·1 cm and 9·1 cm meshes.

Olsen has shown that the weighted mean proportion of each length group within the range of overlap will give the more accurate representation of the length frequency of the population. The weighted mean proportion, p, of any length group, l, within the range of two gill nets A and B is given by

$$pl = \frac{\dfrac{ACl}{\sum ASl} + \dfrac{BCl}{\sum BSl}}{\sum \left| \dfrac{\dfrac{ACl}{\sum ASl} + \dfrac{BCl}{\sum BSl}}{ASl + BSl} \right|}$$

The accuracy of the corrected length frequency distribution of each mesh size can then be compared against the weighted mean distribution by the chi-

Table 6

Chi-square tests of the accuracy of adjusted length-frequency distributions based upon selection curves calculated from Holt's theory and algebraically

Length (cm)	Holt's Method Weighted mean proportion	Proportion 8·1 cm	Proportion 9·1 cm	Algebraic Method Weighted mean proportion	Proportion 8·1 cm	Proportion 9·1 cm
20·5	·188	·185	·197	·213	·213	·205
21·5	·197	·194	·188	·194	·194	·188
22·5	·330	·293	·340	·311	·277	·331
23·5	·297	·329	·275	·281	·316	·277
Mean retention L (cm).....		20·8	23·6		21·0	23·5
Standard deviation.....		1·20	1·20		1·16	1·16
χ^2		1·11	0·14		0·81	0·18
		11·2 cm	12·3 cm		11·2 cm	12·3 cm
27·5	·282	·272	·375	·270	·288	·269
28·5	·274	·258	·230	·250	·271	·213
29·5	·213	·215	·177	·203	·219	·201
30·5	·108	·116	·094	·111	·109	·126
31·5	·090	·095	·084	·108	·081	·126
32·5	·042	·044	·040	·058	·032	·065
Mean retention L (cm).....		29·2	31·9		29·3	31·7
Standard deviation.....		1·48	1·48		1·57	1·57
χ^2		0·15	4·34		2·27	1·14

square test where the numbers of degrees of freedom is one less than the numbers of length groups over which the comparison is being made.

The comparison should be carried out on data not used in the original calculation but this has not been possible with the data for *T. esculenta*. Chi-square tests have been carried out on the corrected distributions obtained from selection curves based on parameters calculated by HOLT's method, and by the algebraic method.

The results are given in Table 6 and show that the algebraic method gives a slightly more accurate correction.

Selection curves were not fitted in detail to the data for 9·6 cm and 10·2 cm meshes because the information is inadequate where the distributions depart from normality. An approximate fit can be obtained for both meshes on the assumption that the 9·1 cm and 12·3 cm mesh selection curves are normally distributed throughout their range. For example, in the 9·6/9·1cm mesh comparison the ordinate of the normal distribution of the 9·1 cm mesh is known for each length group and the numerator can then be calculated using the observed catch ratio.

Discussion

An initial step in the investigation of the dynamics of a fish population is to determine the selection characteristics of the gear from which data are to be obtained for future assessments.

The theory of the determination of the selection characteristics of nylon gill nets has been described by HOLT (1957) and applied by a number of workers

who have shown that for some species the selection curve of a gill net may not be truly normal.

This has been shown to be true for *T. esculenta* also. Over a greater part of the selection range the fish catches of a given mesh size are normally distributed but at the limits of the selection range the numbers of fish caught are greater than would be predicted from the normal distribution. This is shown by the sigmoid form of the regression of the logarithm of the catch ratios of the mesh comparisons, and is probably caused by the entangling powers of synthetic fibres.

For *T. esculenta* the catch distributions of 9·6 cm and 10·2 cm nylon nets show a marked departure from the normal distribution. Data for the girth/length relationship show that in the length range taken by these nets there is a trend in the standard deviation of the length for a given girth which may be responsible for this asymmetry. The biological explanation of this trend is not known but it should be noted that fish mature for the first time in the length range of these mesh sizes.

The parameters of the selection curves of 8·1 cm, 9·1 cm, 11·2 cm, and 12·3 cm meshes are calculated by HOLT's method and also by an algebraic method which is of value in certain circumstances when the length range of a species that is available in one habitat is so restricted that it is not possible to fish an extensive range of mesh sizes. OLSEN's method (OLSEN, 1959) of adjusting gill-net catches to obtain the true relative proportions of different length groups in the population shows that the two methods give closely similar results.

Even so the present conclusions on the selectivity of nylon gill nets for *T. esculenta* can only be regarded as a first approximation when applied to data from commercial fisheries because several brands of net are in common use, each of which will have unique characteristics.

It should also be noted that there are other serious sources of bias in such an analysis which cannot at present be evaluated. It has been shown by KIMSEY (personal communications) that in Lake George the selection curves for *Tilapia nilotica* taken in 12·3 cm set gill nets have a slightly higher mean retention length than the distribution of fish caught in 12·3 cm gill nets into which the fish have been driven by beating. A partial explanation lies in the lifting of the latter immediately after the drive such that a number of fish are taken which are only "loosely gilled" and which would eventually have escaped from set nets. This "loose gilling" has been observed in fish taken from set nets for marking experiments.

Furthermore, routine recordings of the length-frequency distributions of commercial fish catches have shown that at periods of the influx of recruits to the exploited stock, larger numbers of small fish are captured than would have been expected from the selection characteristics of the gear. This is believed to result from shoaling behaviour of fish at these sizes. At other times fish are distributed over the breeding grounds and might be expected to encounter the gear at random.

Acknowledgements

My thanks are due to Mr. R. J. H. BEVERTON and Mr. J. A. GULLAND of the Fisheries Laboratory, Lowestoft, for their criticism of the manuscript. I also wish to thank Mr. D. ILES of JFRO Nyasaland and my colleagues of EAFRO for many helpful discussions during the preparation of this paper.

Summary

1. The selection characteristics of nylon gill nets for *Tilapia esculenta* have been analysed using HOLT's method of comparing catches at successive length groups in gill nets with overlapping selection ranges.

2. An error due to omission of a figure from the original transformation of the formula for a normal distribution, as published in HOLT's paper, has been noted.

3. It is shown that the length frequency distributions for *T. esculenta* of gill-net catches from gill nets of different mesh size are normal over the greater proportion of their range.

4. The fit of the theoretical curve to the observed data, using HOLT's method, is compared to the fit of a theoretical curve derived from an algebraic extension of HOLT's method for use with species whose biological characteristics are such that only a limited number of gill-net mesh sizes may be used to exploit the population.

APPENDIX I

The Derivation of Expressions (1) and (3) in the Text

From HOLT's General Theory $\sigma = \sqrt{\dfrac{B^L M^2 - A^L M^2}{2a}}$

Expanding this expression $\sigma^2 = \dfrac{(B^L M - A^L M)(B^L M + A^L M)}{2a}$

Now $A^L M + B^L M = 2^a/_b$ and $B^L M = 2^a/_b - A^L M$

$$\therefore \sigma^2 = \frac{(2^a/_b - 2A^L M)\, 2^a/_b}{2a}$$

$$\sigma^2 = \frac{(2^a/_b)^2 - 4^a/_b\, A^L M}{2a}$$

$$A^L M = \frac{(2^a/_b)^2 - 2a\sigma^2}{4^a/_b}$$

Expression (1)

If two pairs of gill-net units 1 and 2 are compared $B^L M_1 = A^L M_2$
and since $B^L M_1 = 2^{a_1}/_{b_1} - A^L M_1$
and $\sigma_1 = \sigma_2$
we have from Expression (1)

$$2^{a_1}/_{b_1} - \left[\frac{(2^{a_1}/_{b_1})^2 - 2a_1\sigma^2}{4^{a_1}/_{b_1}}\right] = \frac{(2^{a_2}/_{b_2})^2 - 2a_2\sigma^2}{4^{a_2}/_{b_2}} \qquad \text{(i)}$$

$$\therefore 8^{a_1}/_{b_1}\, {}^{a_2}/_{b_2} - 4^{a_2}/_{b_2}\left[\frac{(2^{a_1}/_{b_1})^2 - 2a_1\sigma^2}{4^{a_1}/_{b_1}}\right] = (2^{a_2}/_{b_2})^2 - 2a_2\sigma^2 \qquad \text{(ii)}$$

$$\therefore 8^{a_1}/_{b_1}\, {}^{a_2}/_{b_2} - \frac{{}^{a_2}/_{b_2}}{{}^{a_1}/_{b_1}}\left[(2^{a_1}/_{b_1})^2 - 2a_1\sigma^2\right] - (2^{a_2}/_{b_2})^2 = -2a_2\sigma^2 \qquad \text{(iii)}$$

$$\therefore 8^{a_1/b_1}{}^{a_2/b_2} - \frac{a_2/b_2}{a_1/b_1}(2^{a_1/b_1})^2 + \frac{a_2/b_2}{a_1/b_1} 2a_1\sigma^2 - (2^{a_2/b_2})^2 = -2a_2\sigma^2 \qquad \text{(iv)}$$

$$8^{a_1/b_1}{}^{a_2/b_2} - \frac{a_2/b_2}{a_1/b_1}(2^{a_1/b_1})^2 - (2^{a_2/b_2})^2 = -2a_2\sigma^2 - \frac{a_2/b_2}{a_1/b_1} 2a_1\sigma^2 \qquad \text{(v)}$$

$$8^{a_1/b_1}{}^{a_2/b_2} - \frac{a_2/b_2}{a_1/b_1}(2^{a_1/b_1})^2 - (2^{a_2/b_2})^2 = -2\sigma^2\left(a_2 + \frac{a_2/b_2}{a_1/b_1} a_1\right) \qquad \text{(vi)}$$

$$\therefore \sigma = \sqrt{\frac{\frac{a_2/b_2}{a_1/b_1}(2^{a_1/b_1})^2 + (2^{a_2/b_2})^2 - 8^{a_1/b_1}{}^{a_2/b_2}}{2\left(a_2 + \frac{a_2/b_2}{a_1/b_1} a_1\right)}} \qquad \text{Expression (2)}$$

Let $p = {}^{a_1}/_{b_1}$ ($^a/_b$ of Gill Net comparison 1)

and $q = {}^{a_2}/_{b_2}$ ($^a/_b$ of Gill Net conparison 2)

$$\text{Then} \quad \sigma = \sqrt{\frac{\frac{q}{p}(2p)^2 + (2q)^2 - 8pq}{2\left(a_2 + \frac{q}{p} a_1\right)}} \qquad \text{Expression (3)}$$

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The Estimation of the Effect on Catches of Changes in Gear Selectivity

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An important part of the present work of fisheries research workers is to estimate the effects on catches both immediate and long-term, of changes in selectivity of the gear being used, in particular of changes in the mesh size of trawls. Such effects can of course be estimated by the use of any of the general population models (cf. Beverton and Holt, 1957). However, application of minimum trawl mesh sizes should, for both practical and administrative needs, be as uniform as possible; that is, if a fleet of trawlers is fishing several species or in several areas, the minimum mesh size should, for ease of administration, be the same for all species or all areas. This means that a minimum mesh size will often at least be considered as a possibility even when the scientific data are far too scanty to provide adequate estimates of all the parameters required in the general population models. Further, these parameters, as generally estimated, refer to the main bulk of the fished population, while the effects of changes in selection are determined by the values for the smallest fish caught, which may well be different. In particular the values of fishing mortality, and possibly also natural mortality, are likely to be different for different sizes of fish. This paper will be concerned with methods of assessing the effect of mesh changes with limited data, but data which will not be unduly biassed if the fishing or natural mortalities in the selection range are different from those in the main fished stock. Such methods will of course not be directly applicable in assessing changes resulting from alteration in fishing effort.

Allen (1953) has shown that if the size of first capture (i. e. the smallest size at which the fish are retained by the gear in use) has been properly chosen so as to give the greatest catch with the existing fishing mortality, then the condition satisfied is that, (with some changes from his notation)

$$W_c = E\bar{W}$$

where W_c = weight at size of first capture

$\bar{W}$ = mean weight of fish in the catch greater than W_c

E = proportion of fish of size W_c which are ultimately caught.

In the simple constant parameter case $E = {}^{F}/_{F+M}$. The equation shows

that the weight of fish released is equal to the "expected" weight when caught later in life. In this equation $\bar{W}$ and W_c can be readily determined from observations of the present catches, but the value of E is not so easy to determine with any precision. The equation may then be re-written in a form which may be more useful,

$$E = W_c/\bar{W}$$

or, in terms of length, assuming $W \times l^3$

$$E = \bar{l_c^3}/\bar{l^3}$$

when $\bar{l^3}$ denotes the mean value of l^3, which will be rather greater than $(\bar{l})^3$, the cube of the mean value of l.

This can also be re-written as an inequality, giving the condition that E has to satisfy for an increase in size of first capture to give an increase in catch, viz.

$$E > W_c/\bar{W} = \bar{l_c}/\bar{l^3}$$

In those fisheries for which no good estimate of E can be obtained — and these are very numerous — the right hand side of this inequality can still be readily calculated, giving a limiting value of E ($= E_L$). A range of likely values of E may be judged by comparison with similar but better studied fish stocks, or by the degree of development of the fishing on the stock, etc., and it may often happen that the limiting value, E_L, lies outside this range. For example if E_L is greater than any likely value of E, increasing the size of first capture is most unlikely to increase the catch. Thus reasonably reliable statements about the desirability or otherwise of an increase in size of first capture can not infrequently be made.

When recruitment to the exploited stock takes place over a range of sizes rather than abruptly at one size — e. g., mesh selection by trawls — then the values used for W and W_c have to be slightly modified, so that, following ALLEN's original development,

W_c = average weight of fish released following a small increase in mesh size and as before

$\bar{W}$ = average weight of fish in the catch.

The value of W_c corresponding to the mesh size, m_1, in use (say ${}_1W_c$) can be determined at once from the present catch and the difference in selection between meshes m_1 and $m_1 + dm$; it is the average size of fish caught by mesh m_1 but released by mesh $m_1 + dm$. For any larger mesh m_2, the catches with it, and hence ${}_2\bar{W}$, must first be determined from the difference in selectivity of meshes m_1 and m_2, and then ${}_2W_c$ determined as the average size of fish caught by m_2 but released by $m_2 + dm_2$.

While a qualitative statement as to whether or not an increase in size of first capture will give an increased catch is useful, a quantitative assessment of the size of such increase following any given increase in size of first capture is usually needed. Such a quantitative assessment can be considered in two stages: the assessment of the immediate effect of a change in selectivity, and that of the long-term effect, after the population has settled into the new steady state. For the former the essential information is the size distribution of the present catches (the problem of discards, and the distinction between catch and landings, is ignored here, but will be dealt with later in this paper),

and the selectivity of the present and proposed new gears. Then for any size group we may write

$_tC_1$ = numbers caught with the present gear
$_tC_K$ = numbers caught with the new gear immediately following the change
W_t = average weight of fish in the size group
$_tS_1$ = proportion retained by present gear
$_tS_2$ = proportion retained by the new gear

Of these quantities $_tS_1$ and $_tS_2$ may in principle be directly estimated by the usual selectivity experiments — though there is often a practical problem in determining what precisely is the average effective mesh size in use. Shrinkage of new nets and subsequent stretching makes the mesh size when fishing very different from the nominal size when new, while chafing gear may make the effective mesh very different again. Also the average mesh size in use in a regulated fishery is unlikely to be the same as the minimum legal size, and will generally be rather larger. $_tC_1$ may be best estimated directly from samples of the commercial catches.

If the pattern and intensity of fishing remain unaltered, then, because the population will not have had time to change, the only factor which could change the catches is the selectivity, and $_tC_K$ can be directly estimated as

$$_tC_K = {}_tC_1 \times {}_tS_2/{}_tS_1$$

Then we have, adding for all length groups,

total catch in numbers with small mesh, $C_1 = \Sigma_t C_1$
immediate catch in numbers with large mesh, $N_K = \Sigma_t C_2$
catch in weight with small mesh, $Y_1 = \Sigma_t C_1 W_t$
immediate catch in weight with large mesh, $Y_K = \Sigma_t C_2 W_t$
number of fish released, $N_R = C_1 - C_K$
immediate loss in weight, $Y_R = Y_1 - Y_K$

In estimating the long-term effect of the mesh change we will at first assume that the selection is knife-edge, such that at present no fish with lengths less than l_1 are caught, but that all fish larger than l_1 are exposed to the full fishing mortality. Similarly, for the new mesh all fish are retained above length l_2. Suppose that the ages corresponding to l_1, l_2 are t_1, t_2; then the change in selectivity will not alter conditions among fish older than t_2, so that the numbers in the population and in the catches will be proportional to the numbers of fish reaching age t_2. That is, if

Y_2 = long-term yield above t_2 after selectivity change
N'_2 = numbers reaching age t_2 with present selectivity
N_2 = numbers reaching age t_2 when population has reached a steady state with the new selectivity

then $Y_2/Y_K = N_2/N'_2$, and the problem is essentially to estimate the latter ratio, (i. e., the increase in numbers of fish reaching the higher age at first capture).

HOLT (1958) has obtained a simple expression for this in terms of the fishing mortality, for if N_1 = numbers of fish reaching age t_1, which will be the same for both conditions, then in the usual notation

$$N'_2 = N_1 e^{-(F+M)(t_2-t_1)} \qquad N_2/N'_2 = e^{F(t_2-t_1)}$$
$$N_2 = N_1 e^{-M(t_2-t_1)} \quad \text{and} \quad Y_2 = Y_R\, e^{F(t_2-t_1)}$$

This gives a simple compact formulation in terms of only two quantities — the fishing mortality and the time interval. However this simplicity is in appearance only, if the fishing mortality is not the same for all ages of fish, e.g., due to the different distribution of the smaller fish. Then, following HOLT, the ages t_1, t_2 must take into account the pattern of recruitment and are the mean resultant selection ages for the two selectivities, obtained from the resultant selection ogive (the product of the recruitment and selection curves), c. f. BEVERTON and HOLT (1957), Figure 8.3. If recruitment occurs sharply at age t_r, and t'_1, t'_2 are the ages corresponding to the two gear selectivities, then

$$t_1 = \text{greater of } t_r,\ t'_1$$
$$t_2 = \text{greater of } t_r,\ t'_2$$

Hence $e^{F(t_2-t_1)}$ will be less than $e^{F(t'_2-t'_1)}$ unless t_r is less than t'_1, i. e., unless recruitment is complete before gear selection occurs, and will in fact become zero when t_r is greater than t_2. Thus estimating the time interval solely from gear selectivity could overestimate, perhaps seriously, the increase in long-term catch.

Alternatively, we can see that $N_2 = N'_2 +$ those of the fish caught by the small mesh, but released by the larger mesh, which survive to age t_2. If the time interval t_1 to t_2 is small, then the reduction due to natural mortality in this period is small and, neglecting this mortality,

$$N_2 = N'_2 + N_R$$

Also if a proportion E^* of the fish reaching age t_2 are caught ($E = F/F + M$ in the usual constant parameter case), then

$$C_2 = EN_2,\ N_K = EN'_2,$$
$$\text{hence } C_2 = N_K + EN_R$$
$$\text{and } C_2/N_K = 1 + EN_R/N_K$$
$$\text{and therefore } Y_2/Y_K = 1 + EN_R/N_K$$

This gives an estimate in terms of quantities N_K and N_R, which are directly observable from samples of the present catch, and the simple quantity E. This latter is not an instantaneous rate, but is the probability of capture during the whole of the fishes' subsequent life, and thus is not greatly biassed if in fact the fishing mortality of the small fish is not the same as that of the larger fish.

A closer estimate can be obtained by allowing for the natural mortality among the N_R fish released, that is

$$N_2 = N'_2 + N_R e^{-Mt'}$$

where t' is the average time between being released and reaching age t_2. If fish are released uniformly between ages t_1 and t_2, then $t' = \frac{1}{2}(t_2 - t_1)$, and this is probably the most useful approximation. Strictly, if fish are fully recruited before t_1, then slightly more fish will be released in the early part of the interval, so that t' will be rather greater than $\frac{1}{2}(t_2 - t_1)$, but it may be that recruitment is still taking place between t_1 and t_2, in which case more fish would

*E in the standard notation is the "exploitation rate" or "expectation of death by capture", referred to some defined time interval, and is therefore equal to $(1 - S)\ F/Z$. Here S is the fraction of those fish present at the beginning of a time period which survive to the end of that period. The term "exploitation rate" is usually applied to the *annual* expectation, but in this paper E is expressed on a life-time basis (so $S = 0$) and is referred to throughout as the "expectation of capture". It may be noted that RICKER (1958) distinguishes "rate of exploitation" (expectation of capture) from "rate of utilization" (annual expectation of capture and subsequent landing).

be released in the later part of the time interval, and t' would be less than $\frac{1}{2}$ $(t_2 - t_1)$.

Apart from the approximation to t' in the second method, the two forms are clearly closely related, and this relation may be shown by expanding the two expressions. For the first we have

$$N_2/N'_2 = e^{F(t_2-t_1)}$$

or, writing $t_2 - t_1 = t$, and expanding,

$$= e^{Ft} = 1 + Ft + \tfrac{1}{2}(Ft)^2 + 0(t^3), \quad \ldots\ldots\ldots\ldots\ldots (1)$$

where $0(t^3)$ denotes terms of the order of t^3 and smaller; for the second

$$N_2/N'_2 = 1 + E\frac{N_R e^{-Mt'}}{N_K} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots (2)$$

Expressing the right hand side of (2) in terms of F and M,

$$E = F/F + M$$

$$N_R = N_1 \frac{F}{F+M}(1 - e^{-(F+M)t})$$

$$N_K = N_1 e^{-(F+M)t}\frac{F}{F+M}$$

Hence $N_2/N'_2 = 1 + \dfrac{F}{F+M} e^{(F+M)t}(1 - e^{-(F+M)t})\, e^{-Mt'}$

$$= 1 + \frac{F}{F+M}[1 + (F+M)t + \tfrac{1}{2}O(t^2)]\,[(F+M)t - \tfrac{1}{2}(F+M)^2t^2 + O(t^3)]\,[1 - Mt' + O(t^2)]$$

$$= 1 + F[1 + (F+M)t]\,[t - \tfrac{1}{2}(F+M)t^2](1 - Mt') + O(t^3)$$

$$= 1 + Ft + [\tfrac{1}{2}F^2 + FM(\tfrac{1}{2} - \frac{t'}{t})]t^2 + O(t^3) \quad \ldots\ldots\ldots\ldots (3)$$

A comparison of expressions (1) and (3) shows that the first two terms are identical, and also the third, if t' is put equal to $\frac{1}{2}$ t; in fact, for constant F and M

$$t' = \frac{t - \dfrac{1}{F+M}(1 - e^{-(F+M)t})}{1 - e^{-(F+M)t}}$$

which expanded in terms of t becomes

$$\tfrac{1}{2}t - \tfrac{5}{12}(F+M)t^2 + O(t^3)$$

Selection over a Range of Sizes

Both methods can be applied without formal modification to the more realistic situation in which selection occurs over a range of sizes. Thus the differences between an assumed knife-edge selection and the real selection ogive have been studied by GULLAND (1957), who showed that there was usually little difference, and in particular the assumption throughout of the simple knife-edge selection gave a good estimate of the effect of change in mesh size. The present situation is rather different, in that the first step of calculating the immediate effects of using a larger mesh is based on the true selection curve, and only the long-term change is based on the assumption of knife-edge selection. The errors involved are likely to be rather larger, though still small. The biggest errors are likely to occur when a large proportion of the catch is

taken within the selection range of the larger mesh. Thus in the first method, the factor e^{Ft} will give the correct increase for numbers of fish above the 100% retention size of the larger mesh, but the numbers of fish within the selection range will not have increased quite so much, so that the increase of the total catch will be slightly overestimated.

In the second method, on the other hand, it is assumed that of the fish that are released, those that are caught later will have the same size composition as the retained catch. In fact some fish at the top of the selection range will, when released, be bigger than the smallest fish in the retained catch. Thus the average size of the released fish, at the time of subsequent capture, will be greater than the average size in the retained catch. The method therefore underestimates the actual increase in weight, but not in number caught. This is clear if we write equation (2) as

$$Y_2/Y_K = C_2/N_K = N_2/N'_2 = 1 + Ee^{-Mt'}\frac{N_R}{N_K} \quad \ldots\ldots\ldots\ldots\ldots\ldots (4)$$

$$\text{or} \quad Y_2 = Y_K + Ee^{-Mt'} N_R \frac{Y_K}{N_K}$$

$$= Y_K + Ee^{-Mt'} N_R \bar{W}_K$$

where $\bar{W}_K$ is the average weight in the retained catch.

Now, $Ee^{-Mt'} N_R$ is the number of the "released" fish which are subsequently caught by the larger mesh, and if $\bar{W}_2$ is their average size when caught, $\bar{W}_2$ is greater than $\bar{W}_K$, and the true long-term catch with the large mesh is

$$Y_2 = Y_K + Ee^{-Mt'} N_R \bar{W}_2 \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots (5)$$

The methods may be best illustrated and compared by using a hypothetical example (see Table 1). This example has been taken to bring out as far as possible the shortcomings of the various methods, and should therefore be treated as an unusually unfavourable situation. The computations have for ease been made in terms of age-groups rather than size groups, but the steps in calculation are formally the same. The latter type of data will be the more common in practice. Values of fishing mortality and natural mortality of 0·2 and 0·1 respectively have been used. Recruitment to the fishery is assumed to take place over a wide range of sizes; this is given in the third column of Table 1, where q_R denotes the proportion of the total number of fish of that age which are exposed to fishing; e. g. for age-group 7 $q_R = 0{\cdot}55$, so that apart from gear selection the potential fishing mortality on these fish is $0{\cdot}55 \times 0{\cdot}2 = 0{\cdot}11$. The selectivities for the old and new gears are given in columns 4 and 5, which show that while all fish of age 7 are retained by the old mesh, only 30% are retained by the new mesh, i. e. the fishing mortalities caused by the two gears are 0·11 and 0·033 respectively. The numbers caught in each age-group by the two gears were calculated by the precise formulae, using the known mortality rates for each year, and these precise figures are given in columns 7 and 10. In any practical situation the known quantities would be the present catch (column 7) and the selectivities (columns 4 and 5). From these the immediate catch following the increase in mesh, (column 9), and the numbers of fish released (column 8) can be calculated at once. The total numbers and weight of the fish in the original catch, respectively released and retained by the larger mesh, are easily obtained as the appropriate column totals, and the sums of products of these columns and the weights given in column 2. In practice, if

Table 1

Hypothetical example of a fished population to illustrate methods of assessment

(For full explanation see text)

Age	W	q_R	S_1	S_2	S_2/S_1	C_1	N_R	N_K	C_2
2	10	0·05	0	0	0	0	0	0	0
3	12	0·10	0·05	0	0	0	0	0	0
4	14	0·15	0·30	0	0	62	62	0	0
5	17	0·25	0·70	0	0	234	234	0	0
6	20	0·40	0·95	0·05	0·053	470	445	25	25
7	24	0·55	1·0	0·30	0·300	533	373	160	181
8	28	0·70	1·0	0·70	0·70	542	163	379	471
9	31	0·85	1·0	0·95	0·95	510	26	484	612
10	34	0·95	1·0	1·0	1·0	431	0	431	552
11	37	1·00	1·0	1·0	1·0	338	0	338	433
12	39	1·00	1·0	1·0	1·0	250	0	250	321
13	41	1·00	1·0	1·0	1·0	185	0	185	238
14	43	1·00	1·0	1·0	1·0	137	0	137	176
15+	46	1·00	1·0	1·0	1·0	393	0	393	504
					Number	4,085	1,303	2,782	3,513
					Weight $\times 10^{-2}$			984	1,248

Actual increase in numbers retained = 3513/2782 = 1·2628
Actual increase in weight retained = 1248/984 = 1·2683
First estimate of $\triangle t = 3\ e^{F\triangle t} = 1{\cdot}82$
True value of $\triangle t = 1{\cdot}28\ e^{F\triangle t} = 1{\cdot}282$

the length-weight data are not available, then a satisfactory alternative is to use the cube of the length as being proportional to the weight. The table shows that the actual gross long-term increases in weight and numbers caught (Y_2/Y_K and C_2/C_K) are 1248/984 = 1·2683, and 3513/2782 = 1·2628 respectively. The slight difference is because the catch in the selection range does not increase by the same amount as the rest, so that the average size of fish in the catch increases slightly.

The estimates that would be made in practice depend on the data available. Using HOLT's method we may assume that for the fully recruited fish the fishing mortality has been accurately estimated as 0·2. The difference in mean selection age of the two meshes is 3 years (5 years to 8 years) which gives a maximum estimate of t, and an estimate $e^{+Ft} = e^{+0{\cdot}6} = 1{\cdot}82$, which is a gross overestimate of the gain. A more satisfactory estimate may be obtained by examining the left hand edge of the age (or length) composition of the present catches; this shows that the mean effective recruitment age is certainly greater than the 5 years given by the present mesh selection curve, and may perhaps be about $6\frac{1}{2}$ years. Correspondingly, the mean selection age with the larger mesh is over 8 years, say $8\frac{1}{2}$ years; this gives $t = 2$ years, $e^{+Ft} = 1{\cdot}49$, which is closer to the true value. In fact the mean selection ages with the two meshes are 7·34 and 8·58 years respectively; this gives $t = 1{\cdot}24$, $e^{Ft} = 1{\cdot}282$. This is the real increase of fish above the selection range of the larger mesh, but is larger than the increase for fish within the selection range, and so gives a slight overestimate of the benefit as a whole.

Using the method of the present paper, we have $N_R = 1303$ and will assume again that accurate estimates of $M = 0{\cdot}2$, $E = 0{\cdot}67$ have been obtained from

the fully exploited population. The first estimate of t obtained from the two selection curves is again 3 years. This gives $e^{-\frac{1}{2}Mt} = 0{\cdot}8607$, so that the number of extra fish reaching the mean retention size of the large mesh is 1121, and the extra number caught $= 0{\cdot}67 \times 1121 = 748$. The catch of the larger mesh is therefore estimated to increase by a factor of $1 + \frac{748}{2782} = 1{\cdot}2689$. This is slightly greater than the true increase in numbers, but almost exactly equal to the increase in weight. This very close agreement is probably mainly a coincidence; more important is the fact that estimates of t which are rather far from the true value will give reasonably close estimates of the benefit: for instance, taking $t = 1$ or 5 years gives values of $e^{-\frac{1}{2}Mt} = 0{\cdot}9512$ or $0{\cdot}7788$, and increases of $1{\cdot}2970$ or $1{\cdot}2431$ – errors of under 3% above and below the true value.

An estimate of t' which may be rather better than $\frac{1}{2}\ t$ may be obtained as the difference between the mean age of the N_R fish, (which is relatively easy to measure in practice) and the mean effective selection age of the larger mesh. This will in general be greater than the mean selection age as measured by mesh selection experiments, to an extent depending on the recruitment pattern. (It may well be difficult to measure in practice.) In the example the mean age of the N_R fish is readily calculated as 6·82 years; the true mean effective selection age of the larger mesh is 8·58 years. Though this value cannot easily be estimated from the data available in practice, the catches of the larger mesh would suggest a value reasonably close to it. This gives a value of $t' = 1{\cdot}76$ years, which is in fact very close to the value of 1·5 years estimated from half the difference in mean selection ages of the two meshes.

Fisheries with more than one Gear

The methods may be directly extended to cover fisheries where more than one gear is used. The number N_R of fish released will be given by the catches and selectivities of only those gears whose selectivity is changed. The number N_K will however depend on the catches of all gears which may later catch the released fish. Generally it will be assumed that the probability of being caught by any particular gear is the same for all fish of the same size, whether they are part of the N_R released fish, or of the N'_2 originally in the stock. An example of possible exceptions is when two gears, e. g. trawls and lines, are fishing slightly different areas; then the fish released by the trawl are, compared with the average fish of their size, more likely to be caught by trawl, and less likely to be caught by line until mixing has taken place.

Assuming that the probabilities are in fact equal, then equation (2) may be re-written, using prefixes T for "trawl" (the selecting gear) and o for other gears, as

$$ {}_TY_2/{}_TY_K = {}_oY_2/{}_oY_K = N_2/N'_2 = 1 + E\,e^{-Mt'}\,\frac{{}_TN_R}{{}_oN_K + {}_TN_K} \quad \ldots\ldots\ldots\ldots \quad (5) $$

where ${}_oN_K$ is the number of fish above the selection size which are caught by the other gear.

In the simplest case the catches of the non-selecting gear are of fish all greater in size than the larger selection size of the selecting gear, and ${}_oN_K$ is equal

to the total catch of the non-selecting gear. In this case no detailed size composition of the catches of the non-selective gear is required — only the average size, which is required to calculate the numbers caught. Clearly, also, any fish caught by the non-selecting gear which are smaller than the lower selection size will not be affected at all by the change in selection, and these will not be included in ${}_oN_K$. Fish within the selection range will be affected, but not to the full extent, and should be only partially included in ${}_oN_K$. The correct weightings would appear to be to write ${}_oN_K$ as the sum of the contributions of the various sizes i

$$ {}_oN_K = \sum_{l_1}^{l_2} p_i \, {}_oN_i + {}_oN' $$

where l_1, l_2 are the two selection sizes
p_i = proportion of the N_R fish smaller than l_i
${}_oN_i$ = number of fish in the i^{th} length group caught by the gear
${}_oN'$ = number of fish greater than l_2 caught by the gear.

An alternative method would be to apply the trawl selection curve to the catches of the other gear. This will give nominal values of ${}_oN_R$ and ${}_oN_K$, and the latter can be used in calculating the long-term effect.

If no detailed data are available about the sizes of fish caught by the non-selecting gear, then some estimate may be made from the trawl catches. Probably the best is to assume that the sizes are the same as those caught by trawls using the larger mesh size. If in fact the fish are larger, then the number of fish in the catch will be overestimated and hence the long-term catches by all gears equally underestimated. If they are smaller, then the catch in numbers will be underestimated. However, some of these fish will presumably be below the selection range, and should not be included in N_K; thus the estimated value of N_2/N'_2 etc. may well be not so far from the true value. Hence the long-term catches by the trawl fleet will be nearly correct, or underestimated, but those by the non-selective gear (because only the part above the selection size will increase), will probably be overestimated.

Discards

The analysis so far has treated catches as being equivalent to landings. In fact numbers of fish, predominantly small ones, are often discarded at sea. If the calculations have been based on catches, then they correctly estimate the effects on catches, and also the long-term effect on landings of fish too large to be discarded. However, the immediate losses to the landings of small fish below the selection size of the larger mesh will be less than the losses to the catches, to the extent that the latter include fish which would have been discarded. If the discarding practice is known in detail, so that for each size of fish the proportion discarded is known, then this proportion can be used to correct each size group in the estimate of the immediate losses to the catches. Hence the immediate losses to the landings can be determined.

More often data on size-composition will refer to landings. The estimate of the immediate effect on landings will therefore be correct, so long as the discarding practice is unchanged (i. e. the fraction of each size group discarded is constant). However, N_R and hence also the long-term increase will be underestimated to the extent that the true number includes fish that would have been

caught and discarded (and presumably killed) as well as fish that would have been landed. The correct value of N_R can be obtained at once from data of the number and sizes of fish discarded and the selection in the usual way. If such data are not available then some reasonable assumption concerning the discards will have to be made.

By ignoring discards, therefore, an unduly pessimistic view of the introduction of a larger mesh would be taken, even if the discarding practice was unchanged. In fact the use of the larger mesh will reduce the absolute numbers of small fish in the catch. This is likely to increase the market demand for the remaining small fish and reduce the work of handling the catch (the main influences on discarding practice) and therefore reduce the proportion of each size discarded. The results obtained by considering discards by the above methods are therefore themselves likely to be too pessimistic. More precise consideration of the extent of change of discard practice following a mesh change is however beyond the scope of this paper.

The analysis so far has assumed that the pattern of fishing after the change in selectivity is the same as that before. For most fish stocks, there are differences, often considerable, in the proportion of small fish in the catches on various grounds. When trawlers (or other vessels) are using a gear which can catch small fish they may tend to fish on the small fish grounds, particularly when the larger and older fish which make up the bulk of the catches on other grounds have been reduced by intense fishing. If the selectivity is changed, so that they cannot catch so many small fish, they will naturally tend to move to grounds where the larger fish predominate. Their catches after the selectivity change will therefore be larger than suggested by the "immediate loss" figures calculated from the catches on the small fish grounds. The long-term catches will also be changed because of heavier fishing than previously on the larger fish, though this will be counteracted by even less fishing than calculated on the small fish around the selection range. What happens in any particular situation requires individual study, especially of the possible alternative fishing grounds for the trawlers, and the catches to be taken from them. Probably even then too much will depend on the particular ideas of the fishermen and of the market for an exact forecast of the changes to be made. Generally, however, such changes in the pattern of fishing, additional to changes in the selectivity of the gear, will not greatly affect the total catch. Of this total the trawlers will take a larger proportion than expected solely from the selectivity change, though smaller than the proportion caught by them before the change. Conversely the non-selecting gear will take a smaller proportion than expected solely from the selectivity change, though larger, both absolutely and relatively, than before the change.

Theoretical situations could however be imagined in which the catch of the non-selective gear was actually greater than following the selectivity change alone, or in which the total catch was substantially increased or decreased.

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Summary

A method of estimating the effect on catches, both immediate and long-term, of changes in the selectivity of the gear, is described.

This depends essentially on knowing the size-composition of the present catches. From this, and a knowledge of the selection curves of the new and old gears, the immediate effect in terms of the numbers of fish retained (N_K), and released (N_R) can be calculated. Of the N_R fish, some ($= N_R e^{-Mt'}$) will live through the average time interval, t', needed to grow to the size retained by the new gear; of these a proportion, E, will ultimately be caught. Thus the immediate catch will be increased in the ratio $N_K : N_K + EN_R e^{-Mt'}$.

The method can be easily extended to cover fisheries in which more than one gear is operating, not all of which change their selectivity.

If fish are discarded at sea, the method gives too pessimistic an estimate of increases in size at first capture.

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The Selection of *Clarias mossambicus* (Peters) by Nylon Gill Nets

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Introduction

In several recent papers (Holt, 1957; Olsen, 1959; McCombie and Fry, 1959; Garrod, 1961) the problem of selection by gill nets has been studied. In these papers the selection curve, either theoretical or observed, has been symmetrical, or nearly so. Data have been collected by the Joint Fishery Research Organisation over the past few years of catches by various sizes of gill nets of several African freshwater fishes. For most of these the shape of the length-frequency curves of the catches of any one net suggested that the corresponding selection curve was nearly symmetrical. However, the catches of the catfish, *Clarias mossambicus* (Peters) had a markedly asymmetrical length-frequency distribution. The lengths of fish caught in 3 inch, 4 inch, 5 inch, and 6 inch gill nets are shown in Figure 1. While a full analysis of the selection of this and other species (including collection of further data of catches using intermediate sizes of gill nets ($2\frac{1}{2}$ inch, $3\frac{1}{2}$ inch, and $4\frac{1}{2}$ inch)) has yet to be made, the preliminary analysis of the selection curve for *Clarias* is presented here for comparison with selection of other species in other parts of the world.

Methods

The fish were caught in routine nettings, using a fleet of 5 nets of 2 inch, 3 inch, 4 inch, 5 inch, and 6 inch (5·1, 7·6, 10·2, 12·7, and 15·2 cm) mesh nylon gill nets in the swamps adjoining Lake Bangweulu (very few fish were caught in the 2 inch net, and they are not analysed here). Mesh sizes were measured with the net diagonally stretched and the measurements refer to the distance

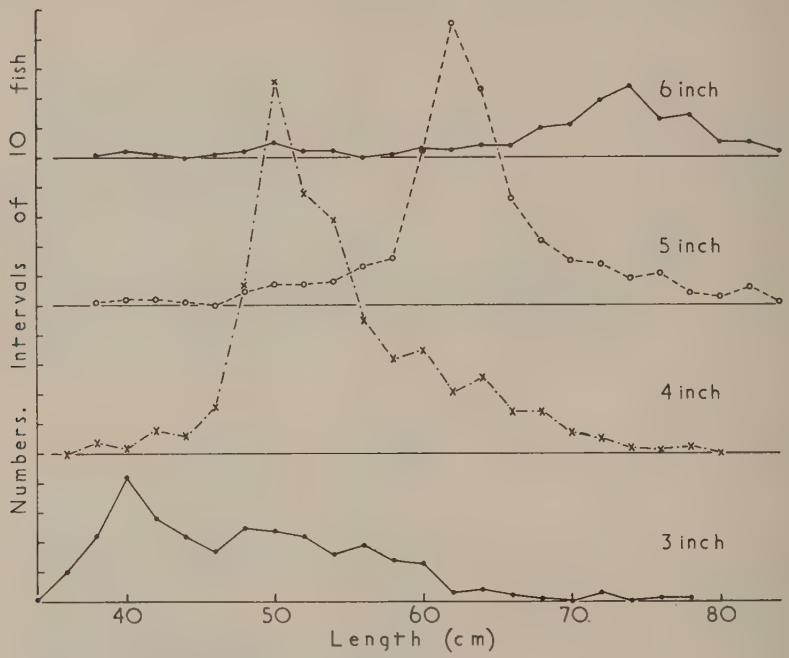

Figure 1. Length composition of catches of *Clarias* by gill nets of various mesh sizes.

between the units. Each net was 100 yards (91 m) long set by the half (i.e. 50 yards (46 m) in the water), and had a depth of about 2·1 m. Altogether 312 sets were made with each net.

Results

The length composition of catches is shown in Figure 1 (grouped in 2 cm intervals, i.e. the 64 cm group contains fish from 64·0–65·9 cm). For the first analysis, following HOLT (1957), the logarithms of the ratios of the catches of each successive pair of nets were calculated; these (for the pairs 3 : 4, 4 : 5, and 5 : 6) are plotted in Figure 2. If the selection curve is normal, and of constant variance, then this plot should be a straight line. In fact the plots obtained do not depart seriously from a straight line where the catches are nearly equal, but for the larger fish the curve flattens out and becomes nearly horizontal. This curvature may appear for many species of fish, but usually only at extreme sizes, and involves an insignificant part of the catch. For *Clarias*, however, this non-linear part of the plot involves an important part of the catch (40% for the 3 inch mesh). It is apparent that the selection curve for *Clarias* is far from being normal.

Following the methods of MCCOMBIE and FRY (1959), the frequency distribu-

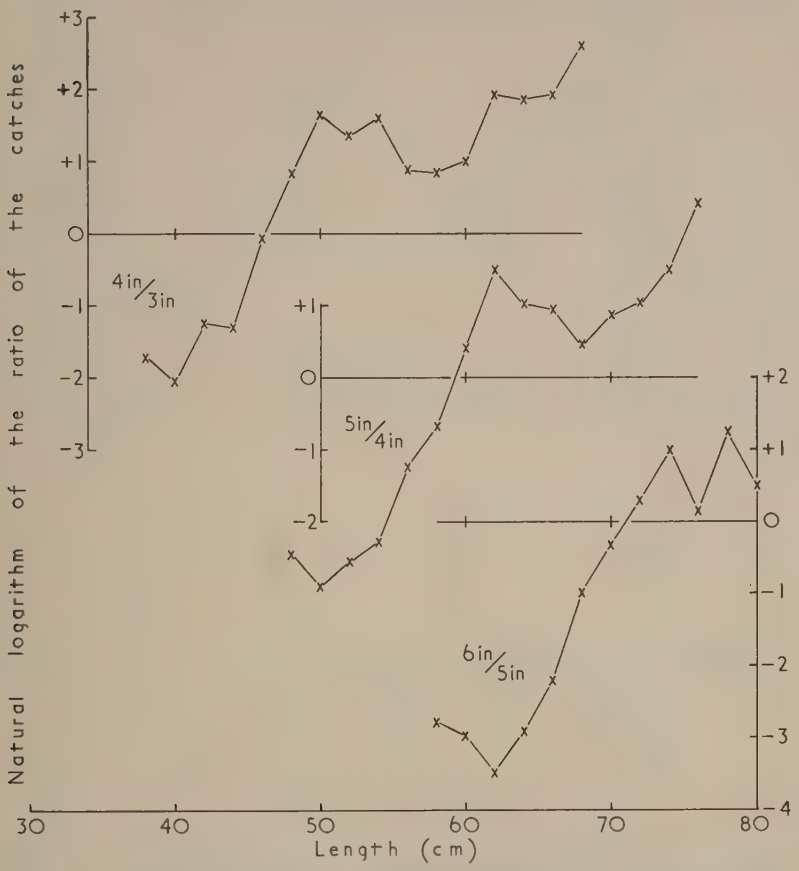

Figure 2. Logarithm of the ratio of the numbers of fish in each 2 cm length group caught by nets of different mesh sizes.

tion of the catches of each net was plotted for each size of fish. The plot for the 60 cm group is shown in Figure 3. McCombie and Fry, using some 10 mesh sizes, were able to define this curve fairly exactly, and used the area under it (or strictly under the frequency curve of log (mesh/girth)), as a measure of the true abundance of the size group in the fished population. With only 4 (or fewer) points the curve was not so well defined, and the maximum of the curve was taken as a measure of the abundance in the population. This is equivalent to assuming that the fishing power of the most efficient mesh for any length group is the same for all length groups, and is consistent with McCombie and Fry's assumption. In drawing the curves there is unfortunately a strong tendency to make the maximum value coincide with one of the observed points; this will tend to under-estimate the maximum value (and therefore the abundance) when the maximum should fall between two observed points.

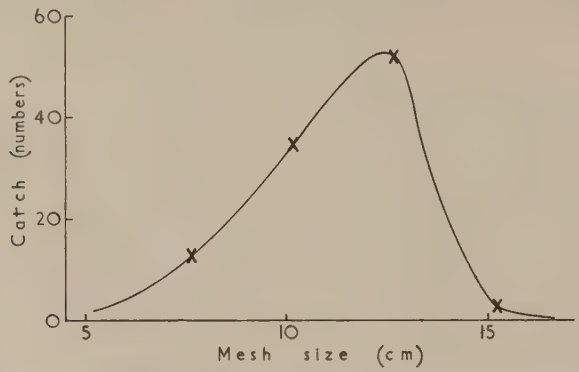

Figure 3. Numbers of fish of the 60 cm length group caught by various mesh sizes, and the smooth curve fitted by eye.

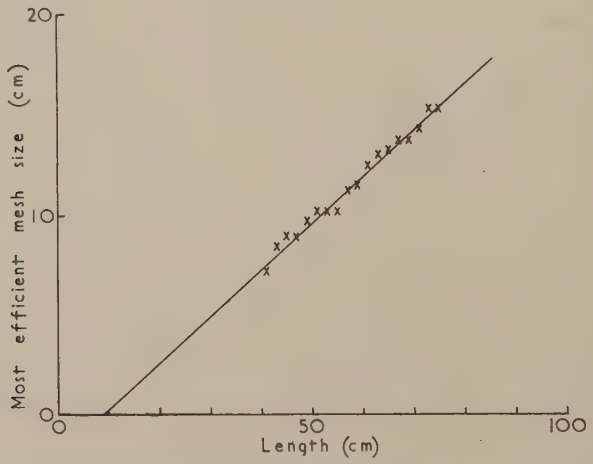

Figure 4. Relation between length of fish and the size of mesh which is most efficient in retaining fish of that size.

In Figure 4 the position of the maximum, i.e. the most efficient mesh size, has been plotted against the length. The points lie closely on a straight line, but this line is not proportional, cutting the axis at a length of 9 cm. While girth measurements were not made as a matter of routine for all the catches, a limited number of pairs of length and girth measurements have been made. For each fish, two measurements of girth were made, one (H) around the head at the operculum, and just in front of the pectoral spines, and the other (M) around the body midway between the operculum and the first ray of the dorsal fin. M is close to the maximum girth, but because of the presence of the pectoral spines, fish are most usually caught at the position H. Both measures are

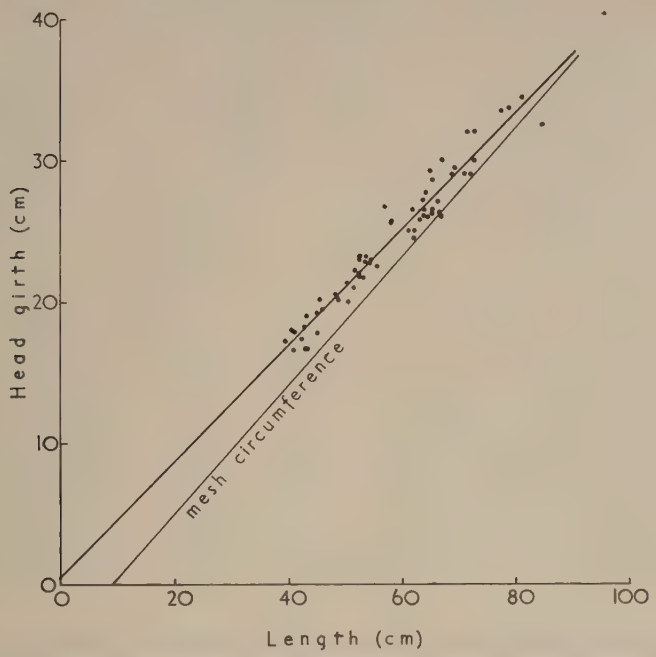

Figure 5. Relation between head girth and length in *Clarias*, showing also the relation between the circumference of the most efficient mesh and length of fish.

closely proportional to length, the lines fitted by least squares being

$$H = 0{\cdot}53 + 0{\cdot}411\ L \text{ and}$$
$$M = 1{\cdot}90 + 0{\cdot}407\ L$$

when L is the length.

The data for head girth are plotted as Figure 5; also shown is the relation between the perimeter of the "best" mesh and length, taken from the line of Figure 4. Over the range of data (40–80 cm) the girth is just a little bigger than the circumference of optimum mesh (at 60 cm $H = 1{\cdot}12 \times$ circumference, $M = 1{\cdot}18 \times$ circumference).

The catches of any length group by each mesh can now be expressed as a proportion of the peak catch of that size, and the mesh size as a proportion of the most effective mesh. These data are plotted in Figure 6; a logarithmic scale has been used for the mesh size, so that the figure is analogous to Figure 3 of McCombie and Fry. Different symbols have been used for the catches of 3 inch, 4 inch, 5 inch, and 6 inch meshes. This curve is strongly asymmetrical and obviously far from normal; for meshes just larger than the optimum the efficiency falls off sharply, but smaller meshes are quite efficient even when very different from the optimum. Though there is not complete overlap of the points for large and small meshes, they all appear to fall on the same curve. Because the points of Figure 6 lie on the same curve whatever the size of mesh,

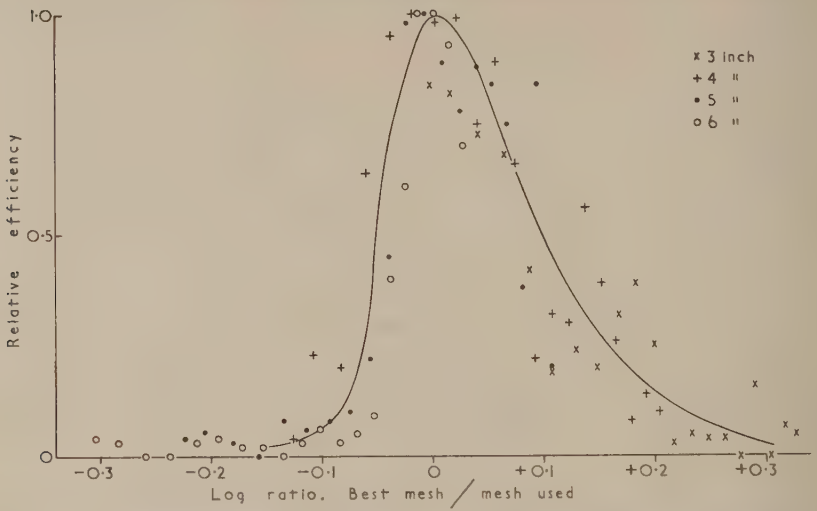

Figure 6. First approximation to the selection curve, expressed as the plot of efficiency of retention for any size of fish against the ratio of best mesh size for that size of fish to mesh size used.

it follows that the efficiency with which any size of fish is caught by any mesh size is determined only by the relative size of fish and mesh, and the efficiency with which that size of fish is caught by the most efficient mesh. If the fishing power of the most efficient mesh is the same for all sizes, then the only factor is the relation between the sizes of fish and mesh (i.e. in effect the perimeter: girth ratio). Thus Figure 6 can also be used to show the efficiency with which a given size of mesh catches fish of different lengths. Used in this way it is clear that, as suggested by the catches shown in Figure 1, a given mesh is inefficient for fish below the optimum size, but will catch fish appreciably larger.

A smooth curve was drawn by eye through the points of Figure 6. From this the relative efficiency with which any size of net catches a given length of fish can be read off at once. This figure can be used to estimate from the catches the relative abundance of each size of fish in the fished population. That is, for a length l, if a mesh size m has a relative efficiency of ${}_mP_l$, and catches ${}_mN_l$ fish, then the abundance in the population is proportional to $\frac{{}_mN_l}{{}_mP_l}$. In practice it is better to pool the results of all meshes, i. e. to take the population abundance as proportional to

$$\frac{\sum_m {}_mN}{\sum_m {}_mP_l}$$

This was used to obtain an estimate of the abundance of each size group better than that obtained earlier as the peak in the catch/mesh size plot.

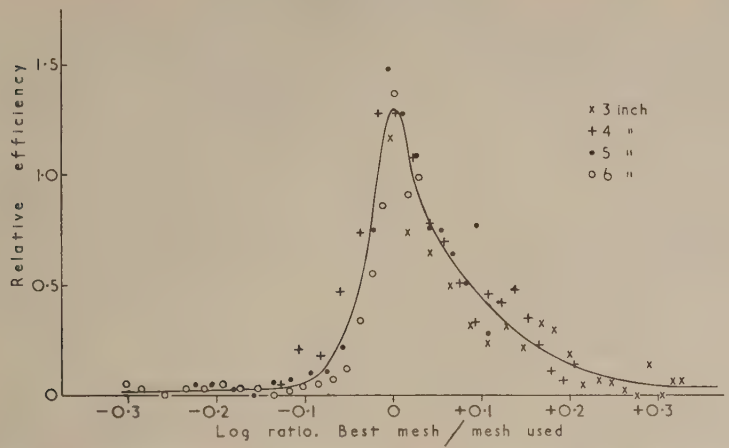

Figure 7. Final approximation to the selection curve, as expressed as the plot of relative efficiency of retention against the ratio of best mesh size to mesh size used.

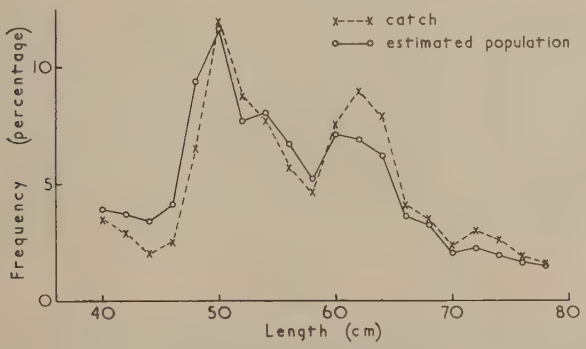

Figure 8. Length composition of the catch, compared with the estimated population in the fished area.

This estimate can in turn be used to give better estimates of the efficiency of any mesh for a given length. As expected, these estimates differ from the earlier ones mainly in increased population abundance, and hence a lower efficiency, when the optimum mesh size falls between two observed mesh sizes. These estimates can now be plotted as in Figure 6 to give a better estimate of the efficiency-size relationship. This in turn can be used to give another estimate of population abundance at each length. Such iterations could be carried on as long as desired, but after the second approximation little change is made either in population size, or efficiency. The efficiency-size curve, (the revised version of Figure 6) obtained after two iterations is shown in Figure 7, which differs but little from Figure 6. In Figure 8 are shown the final estimate of population abundance and the catches at each size, each expressed as a

percentage of the total between 40 and 70 cm. While the catch has modes corresponding to the peak efficiencies for each of the four mesh sizes in use (40, 50, 62, and 72 cm), these have nearly disappeared in the estimate of the fished population, which has one pronounced mode at 50 cm, with a subsidiary mode at 60 cm.

While this "population" curve is not entirely smooth, it probably does come fairly close to the true population curve, and suggests that the selection curves obtained are close to the true curves. In particular the observed departure from symmetry is real, giving a selection curve very different from that observed in other fisheries. This difference may well lie in the shape of the fish, and in the way in which it is caught. Most fish so far studied have the "normal" fish shape, e.g. herring, salmon, whitefish, and the nets act truly as gill nets, the fish being caught behind the gill covers. Compared with these, *Clarias* is a long fish, with a large bony head (the maximum girth occurs at or near to the back of the head). Many fish, particularly the bigger sizes on any one net, are not caught firmly in a single mesh, but are entangled in several meshes; this is probably the cause of the excessively long upper tail of the selection curve.

Summary

Catches of *Clarias mossambicus* by four sizes of gill net were examined. A true index of abundance of each size group was estimated graphically as the mode in the plot of catch against mesh size. From this index the relative efficiency of each mesh size was calculated. An iterative method was used to obtain better estimates of population abundance and mesh efficiency. The efficiency of any mesh seemed to be determined by the ratio of mesh size used: most efficient mesh size for the given size of fish. This selection curve was very asymmetrical, fish much bigger than the peak size being caught, but not fish much smaller. The reason appears to be that large fish become entangled in the meshes.

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Diving Behaviour of Hawaiian Skipjack Tuna

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Introduction

The principal commercial fishery in Hawaii is for oceanic skipjack, *Katsuwonus pelamis* (Linnaeus), a surface-schooling tuna 40–90 cm in length which is captured exclusively by day using pole-and-line with live-bait as chum. In an attempt to increase the catch per unit of effort, the Honolulu Biological Laboratory (HBL), U.S. Bureau of Commercial Fisheries, has begun studies of skipjack behaviour. Major aspects of this subject have been investigated from an underwater observation chamber mounted on the research vessel "Charles H. Gilbert". This blister-like structure, which has been described by STRASBURG and YUEN (1960), is located two metres below the surface in the fishing area at the ship's stern. From this vantage point it is possible to study skipjack behaviour during fishing and at other times.

During July–September 1959, the "Charles H. Gilbert" was engaged in experimental skipjack fishing in Hawaiian waters. Experiments consisted of varying certain fishing conditions such as kind and amount of bait, bait supplements, etc., and in addition to such tests, collecting general information on the behaviour of skipjack. One conspicuous behaviour pattern observed during skipjack fishing was an abrupt vertical movement which we have called "diving". Diving consisted of skipjack vanishing from view in a nearly vertical direction, the fish disappearing at 30–60 m depths. This is of practical importance to the fisherman, for a school which dives frequently requires more bait and yields a smaller catch than a school which remains at the surface.

This report describes a possible cause of skipjack diving. Attention was focused on prey organisms because preliminary observations indicated a relation between prey and behaviour. For example, the fishermen believe that skipjack are conditioned to their natural food, and are difficult to catch with baits differing greatly from this food. In order to evaluate the feasibility of fishing a particular school they examine the spewings of the first few fish caught. The results of their examinations may be used to determine fishing procedure

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or to rationalize a poor catch. If the regurgitated material contains numerous postlarval synodontid fish, the fishermen believe that few skipjack will be caught and extensive bait expenditure is unwarranted.

Methods

Test fishing on the "Charles H. Gilbert" consisted of alternate periods of normal and experimental routine which allowed observers to compare skipjack behaviour under constrasting conditions. Although frequently affecting catch and catch rate, none of the tests caused the tuna to dive, and test effects are therefore ignored in the following account. Records of tuna activity consisted of underwater motion pictures, recorded oral comments by underwater and surface observers, and records of time and catch. Echo-sounders were not used to record skipjack activity primarily because these fish lack a swim-bladder and thus give poor echoes. After fishing, meteorological and water temperature data were obtained, and a sample of the catch was examined for length, sex, and food consumed.

Stomach contents were usually determined for a sample of ten skipjack, but a larger number was examined when an unusual diet was indicated. Dietary items were counted and a rough attempt made to judge their volumes. Excluding bait, 42 food items were encountered, but only ten of these occurred frequently. One of these, unidentified fish remains, was not considered further, but an idea of the importance of the others can be obtained from Table 1.

Identification of the more important food items was necessarily based on the specimens in best condition, and there is a possibility that other species occurred in the damaged material. Fish being eaten were postlarval *Acanthurus* spp. (Acanthuridae), postlarval *Chaetodon corallicola* Snyder (Chaetodontidae), juvenile *Holocentrus lacteoguttatus* Cuvier and Valenciennes (Holocentridae), juvenile *Parupeneus* sp. (Mullidae), and postlarval *Synodus variegatus* (Lacepède) (Synodontidae). Because these fish are littoral as adults, some interest is attached to the fact that their larval and juvenile stages are pelagic. It is thus desirable to explain the procedures used in identification and to briefly describe the specimens.

Acronurus-stage Acanthuridae were identified with the aid of RANDALL's publications (1955, 1956). Meristic characters were used to determine the silvery 25–33 mm chaetodontid postlarvae. Their formulae of dorsal rays XIII, 21 to 23 (usually 22); anal rays III, 18 or 19; pectoral rays 15; and scale rows 31 to 33 are referable only to *Chaetodon corallicola* among the Hawaiian butterfly fishes (GOSLINE and BROCK, 1960; WOODS, in SCHULTZ, *et al.*, 1953; and personal examination of specimens). The squirrel fish were all *Holocentrus lacteoguttatus* (WOODS, in SCHULTZ, *et al.*, 1953; GOSLINE and BROCK, 1960); they were 54–58 mm in standard length, deep blue dorsally, silvery ventrally, and with a bright violet stripe separating these colours. The mullids were also blue and silver, and 53–58 mm in standard length. Four preserved mullids had a single row of caniniform teeth in each jaw and $2-\frac{1}{2}$ scale rows between the lateral line and the dorsal fin interspace. According to GOSLINE and BROCK (1960) they are therefore a species of *Parupeneus*. The descriptions by GIBBS (1959), GOSLINE and BROCK (1960), and SCHULTZ (in SCHULTZ, *et al.*, 1953) were used to identify synodontid postlarvae. The deep-lying dark spots as well as the

Table 1

Diet versus dive-frequency in skipjack

Station number	Number of dives		Number of skipjack eating item (adjusted to sample size 10)								
	Dives ≥ 1 min.	All dives	Acanthuridae	Chaetodontidae	Holocentridae	Mullidae	Synodontidae	Crab megalops	Squid	Stomatopods	Empty
45– 2	0	0	0	0	0	7	0	0	1	0	0
– 3	3	5	0	5·4	0	10	0	4·6	2·3	0·8	0
– 7	1	4	2	10	1	6	0	9	1	1	0
– 8	0	2	1	2	0	0	0	0	5	2	2
– 9	0	0	2	6	0	1	0	0	1	0	0
–23	3	3	0	5	0	0	0	0	0	1	2
–32	1	4	2	1	0	6	1	0	0	0	2
–33	1	2	6	9	1	1	2	1	9	4	1
–34	0	2	2	5	0	4	0	1	2	0	0
–35	1	3	6	10	3	6	2	0	6	4	0
–37	0	1	0	10	0	0	0	2	1·3	0·7	0
–38	1	1	0	10	0	0	1	0	0	1	0
–39	1	5	1	10	0	0	0	3	2	2	0
–44	1	2	1	5	0	2	0	1	3	1	2
–46	2	3	0	3·1	0·8	0	3·8	0	4·6	0·8	0·8
–47	1	1	0	0	0	4	0	0	3	0	5
–49	0	1	0	5	2	0	0	0	4	4	1
–50	5	7	0	2	3	0	4	0	8	0	0
–54	1	1	1	2	2	10	1	0	4	3	0
–57	0	1	1·2	0	0	0·6	0·6	5	1·9	8·8	0
–58	3	5	1	1	2	0	0	1	1	5	1
–59	1	3	0	0·7	3	9·3	0	0	0·7	0	0·7
46– 7	1	1	1·7	0	0	0	0	0	3·3	0·6	4·4
–10	6	8	2	0	9	1	2	0	5	1	0
r, all dives			0·036	−0·061	0·622[2]	−0·020	0·426[1]	0·160	0·242	−0·093	−0·228
r, dives ≥ 1 min..			−0·089	−0·233	0·681[2]	−0·101	0·518[2]	−0·089	0·294	−0·046	−0·087
% of stomachs containing item (305 stomachs examined)			10·5	36·7	9·8	27·5	6·6	10·8	27·9	17·4	12·1
% of schools eating item (27 schools sampled)			51·9	74·1	44·4	55·6	37·0	33·3	85·2	70·4	48·1

[1] Indicates a *p*-value between 0·05 and 0·01. [2] Indicates a *p*-value less than 0·01.

dentition of tongue and jaws showed the 12 preserved specimens to be *Synodus*; one specimen, at least, had the dorsal fin formula of *S. variegatus*. These postlarval lizardfish were large, 55–62 mm in standard length, and were eaten by skipjack captured 3–16 km from shore.

No attempt was made to identify the crabs megalops or stomatopods, but the squid were examined by Robert T. B. Iversen of HBL and identified as *Symplectoteuthis oualaniensis* (Lesson) and *Ommastrephes* sp., both of the family Ommastrephidae.

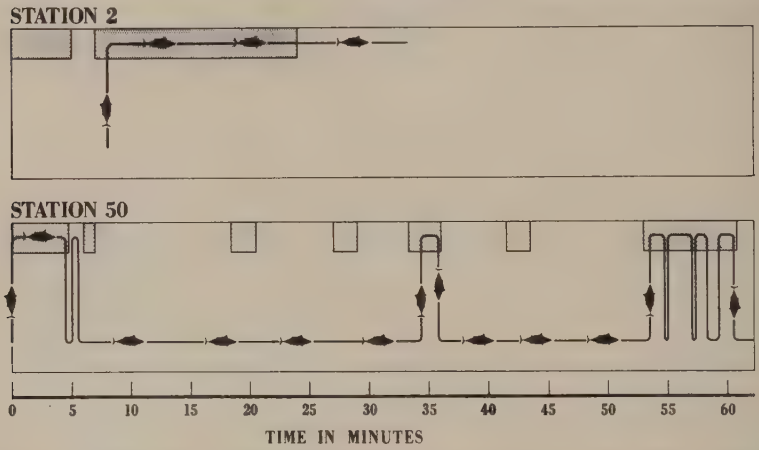

Figure 1. Activity of non-diving and diving schools of skipjack during fishing. Shaded blocks represent chumming intervals, fish figures indicate skipjack activity (surfacing or diving) during this period.

Relation of Diet to Diving

In the most desirable fishing situation a school of skipjack was attracted to the stern with live-bait (attracting fish with live-bait is locally known as chumming) and held there continuously for varying periods of time, usually about 20–30 minutes. With a diving school, the tuna were not only difficult to attract, but after fishing had begun it was periodically interrupted by the fish disappearing into the depths. Diagrammatic representations of extreme cases of these patterns of activity are given in Figure 1. Similar diagrams were prepared for all 24 schools observed in detail, and from these the number of dives per school was determined. A school which remained at the surface until the end of fishing was not considered to have dived, even though it departed in a dive after chumming stopped. Schools leaving the fishing area horizontally were also not considered to have dived, even if they emerged from the depths when re-engaged.

It was evident that diving was the rule rather than the exception (Figure 2). The number of dives per school ranged from 0 to 8, with a mean of 2·7. The tuna were away from the surface as briefly as 3 seconds or as long as 28 minutes. In the case of prolonged dives it was impossible to be certain that only one school was involved. It was felt, however, that only one was present, for the ship remained in the same spot and there were no indications (by birds or surface disturbance) of the approach of other fish. Thirty-three of the 65 dives observed resulted in a surface absence of one minute or more. Most dives were vertical or nearly so, and frequently the fish passed beneath the vessel as they descended. In nearly all cases diving was simultaneous among the hundred or more skipjack visible from the observation chamber.

As explained above, a sample of ten stomachs per school was examined for food. A few larger samples were proportionately reduced to ten for the sake of

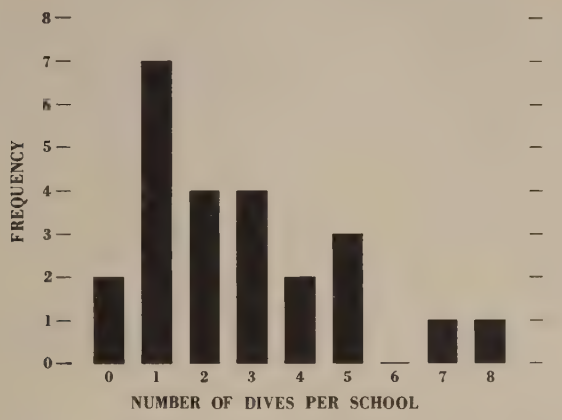

Figure 2. Frequency of diving in Hawaiian skipjack schools.

uniformity. The basic data, together with the results of the correlation analyses used to relate diet and dive-frequency are presented in Table 1. From this it is clear that the consumption of two foods, postlarval *Synodus variegatus* and juvenile *Holocentrus lacteoguttatus*, was significantly related to diving frequency. The correlation analyses treat each food item as if only it had been eaten, and therefore no particular account is taken of those cases, indicated in Table 1, in which *Synodus* and *Holocentrus* occurred together in skipjack stomachs.

Discussion

The food habits of Hawaiian skipjack have been discussed by Welsh (1949) and Yuen (1959), and are generally the same as those of skipjack of Japan (Suyehiro, 1938; Hotta and Ogawa, 1955) and the Philippines (Ronquillo, 1953). Wherever they occur, skipjack prey on small fish, squid, and crustaceans, taking a wide variety of species but also gorging on a few abundant forms. The heterogeneity of their diet has prompted Ronquillo (1953) to state: "These pelagic fishes are seemingly nonselective, that is, they are voracious eaters. They would eat any living organism available."

With such proclivities it is perhaps surprising to find skipjack behaviour influenced by a particular kind of prey. One example of this phenomenon is Yuen's observation (1959) that skipjack feeding on nomeids, thunnids, carangids, and gempylids (all relatively fast swimmers) are caught at a greater rate than skipjack preying on slower-swimming chaetodontids, scorpaenids, molids, and acanthurids. Similarly, skipjack feeding on nomeids, thunnids, and gempylids, but not carangids, are caught for a longer time interval than those eating the slower species.

Other observations on the susceptibility to capture of skipjack schools in relation to their natural food are less clear-cut with respect to diet-induced behaviour. Suyehiro (1938) found that skipjack preying on neritic organisms (mackerel, horse mackerel, spotted shrimp, amphipods, and crab larvae) were

relatively difficult to capture, whereas those taking oceanic food (flying fish, squid, and schizopods) were more easily caught. He surmised that this difference resulted from the relative abundance of food in neritic versus oceanic situations, rather than from a differential response to the food organisms.

It is unlikely that the consumption, *per se*, of *Synodus* or *Holocentrus* produces dyspepsia causing skipjack to flee the surface. Instead it is reasonable to think of them as diving in pursuit of deep-swimming prey whose attractiveness is greater than that of the chum. Thus, a school which is difficult to engage initially could be feeding on an enticing natural food, and one which dives after fishing has begun might be responding to natural food, or to other feeding skipjack, beneath it.

If better use is to be made of chum it is worthwhile to examine the characteristics of attractive natural food. In gross aspect there is little to distinguish *Holocentrus* from *Parupeneus*, the specimens recovered being of the same size, shape, and colour. They seem to have been equally available in 1959 (roughly half of the schools sampled had eaten each), although this is not always the case. YUEN (1959) found over three times as many schools eating holocentrids as mullids in 1956–57. Neither food seems to be preferred over the other, for although YUEN (unpublished data) found holocentrids in six times as many stomachs as mullids, the present data show holocentrids in one-third as many as mullids. Despite these vagaries, the fact remains that consumption of *Holocentrus* was associated with diving whereas consumption of *Parupeneus* was not. In addition to such possibilities as nonrandom sampling or a difference in the depth of occurrence of these two species, there is another possible explanation for this condition. This relates to prey behaviour, about which little is known, yet conceivably the "action" of *Holocentrus* might be attractive to skipjack whereas that of *Parupeneus* might not.

The other fish associated with diving, *Synodus variegatus*, is one of the few skipjack prey species having a prominent colour pattern. Whereas the other food organisms are inconspicuously colourless, blue, or silver, living *Synodus* postlarvae bear a series of large blackish spots on an otherwise unpigmented body. These markings are conspicuous to the human eye but do not suggest a fish-like form owing to the transparency of the intervening flesh. Instead an impression is given of an advancing file of disassociated spots. Judging from the dive data, skipjack detect and react to *Synodus* at distances on the order of 30 m. The immediacy of their response suggests triggering by some releaser, perhaps the spotted pattern of the prey. Apparently only a few *Synodus* are available to a skipjack school, for only 6·6 % of the stomachs examined in this study contained them, and YUEN (unpublished data) found them in only 10 of 573 stomachs. If these fish are as desirable skipjack food as they seem to be, then perhaps their characteristics can be put to human use. Mr. John C. MARR of HBL is presently examining the efficacy of skipjack lures having the shape and pattern of postlarval *Synodus*.

Summary

Observations from an underwater chamber showed that schools of skipjack commonly dive during fishing, leaving the surface for a minute or more on many occasions. Stomach analyses showed that the presence of two prey fish,

Synodus variegatus and *Holocentrus lacteoguttatus*, was significantly related to diving frequency. It was hypothesized that these two species were more attractive than the live-bait used by the fishermen, and that the skipjack dived in pursuit of them. A study of the characteristics of attractive natural food may lead to the development of better bait and lures for catching skipjack.

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Review

A. R. Longhurst. "The Sampling Problem in Benthic Ecology". Proceedings of the N.Z. Ecological Society, **6**: 8–12, 1959.

In his short paper, LONGHURST brings under review some problems of technique which face the quantitative benthic ecologist.

One of the more remarkable facts about this type of investigation is that, with rare exceptions (when special coring techniques have been applied), it is not possible to determine fully the animal content of a standard column of the sea-bed. Only the top 5–10 cm of this column can usually be studied, the strata below this depth remaining to this date a virtually unknown territory. The downward limit of the life-supporting zone has not been established, although that part of the benthos which is generally unavailable for study may contribute significantly to organic production. The differential sampling of the deeper parts of the stratum which is penetrated by grabs, and the lack of control over the action of conventional patterns, as well known frequently means that the investigator is not entitled to state the densities of animals as numbers per unit area.

The generally inefficient sampling characteristics of grabs constitute an important source of error in the estimation of abundance, upon which rests the determination of biomass, production, and mortality, and of the faunal indices which are the zoogeographer's basic statistics. One of my own papers (BIRKETT, 1958) contains a suggestion for overcoming part of this error, which LONGHURST discusses and, quite rightly, rejects because it appears to pose as many problems as it solves. So it does; but while the sampling techniques impose such restrictions as they do there is no perfectly satisfactory answer to the sampling error problem.

LONGHURST discusses at length the faunal indices, which define the population structure in an area. In such matters the zoogeographer, who generally depends on a single collection of samples from any marine area, is at a disadvantage because of the seasonal variations in the fauna, which can bring a completely different part of the fauna into prominence at any time, thus rendering his faunal indices of only temporary value. The numbers of individuals per unit area are subject to extremely rapid fluctuations, due to spatfalls and to mortality. The biomass is not, as hitherto frequently assumed, a static property, but is continually changing, and may be increasing or decreasing. The number of species is a somewhat abstract quantity, and it is curious that the samples in a cumulative array (such as that of HOLMES or JONES, discussed by LONGHURST) may be arranged in any order to give a wide range of asymptotic values for this index; in one arrangement, half the samples contribute no new information

on the species composition, while in another, the number of species continues to rise so rapidly that double the original number of hauls would have revealed an infinity of species.

The limitations of these methods for determining the faunal indices are well appreciated by LONGHURST.

Providing that a species is so dispersed that it occurs in every haul, its density will be adequately estimated, within the limits of error, by any number of samples, from one upwards, and it seems unnecessary to duplicate the labour of taking and sorting the samples. A species which is more dispersed, so that it occurs less frequently, requires more samples for an adequate assessment. Alternatively, if a comparatively rare species were sufficiently important from an economic standpoint, as to warrant assessment, then it is questionable whether the investigator should not abandon the available range of samplers and go in for something which would cover a much larger area — say 1 or 2 m^2; but let it do this to an even depth of penetration. This is certainly not beyond the bounds of feasibility.

It is important that quantitative benthic ecology should be more introspective. The publication of LONGHURST's paper should mark the return of vigour to a once very active branch of fishery science.

L. Birkett

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